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A review of the millipede genus *Pseudodesmus* Pocock, 1887 (Diplopoda, Platydesmida, Andrognathidae) from Vietnam, with descriptions of five new species and notes on its phylogeny

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Abstract

The platydesmidan genus *Pseudodesmus* Pocock, 1887 is reviewed within the scope of the Vietnamese fauna. A total of seven species have been recorded in Vietnam including five new species: *Pseudodesmus bidoup* **sp. nov.**, *Pseudodesmus karstomus* **sp. nov.**, *Pseudodesmus ngoclinh* **sp. nov.**, *Pseudodesmus condao* **sp. nov.**, and *Pseudodesmus irregularis* **sp. nov.** Cytochrome c oxidase I barcodes are provided for these species, and their phylogenetic relationship is discussed.

Key Words

Biodiversity, bio-investigation, COI, phylogeny, Southeast Asia, taxonomy

Introduction

Members of the millipede order Platydesmida represent a taxon of ancient millipedes originally distributed in the former supercontinent of Laurasia (Shelley and Golovatch 2011; Moritz and Wesener 2019). Two distinct habitus types are known: a short body with wide paraterga (= paranota) or a very slender, elongated body with very short (or rarely no) paraterga (Wesener 2015). They have a small and pyriform head, and lack ommatidia. Like other colobognath millipedes, platydesmidan males have simple leg-like gonopods (leg pairs 9 and 10). Due to this and their small size, it is difficult to distinguish platydesmidan species based solely on gonopod characters (Shorter et al. 2018). Most species discrimination is from other characters, for example, antenna, head, legs, coloration, and metazonital shape and sculpture.

The order Platydesmida is currently classified into two families, Platydesmidae de Saussure, 1860 and Andrognathidae Cope, 1869, with 69 described species in 14 genera (Shear 2011; Minelli 2014). Two genera of Platydesmidae only occur in the western Hemisphere, whereas Andrognathidae has 12 genera and 36 species in North America, the Mediterranean Europe, and East and Southeast Asia. Of these, *Brachycybe* (Wood 1864) (3/8); *Pseudodesmus* (Pocock 1887) (9/9); *Symphyopleurium* (Attems 1951) (3/3); and *Yamasinaium* (Verhoeff 1939) (3/3) are presently considered as valid genera from East and Southeast Asia (in parentheses, number of species recorded in Asia/total number of species). Seven other Asian genera described earlier (*Bazillozonium* (Verhoeff 1935), *Sumatronium* (Verhoeff 1935), *Trichozonium* (Miyosi 1953), *Yamasinaium* Takashima, 1953, *Yoshimarium* Takashima, 1953, *Zinaceps* (Chamberlin and Wang

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1953), and *Zinazonium* (Chamberlin 1945) are all junior synonyms according to Hoffman (1980) .

Another genus, *Sinocybe* (Loomis, 1942) (with only one species, *Sinocybe cooki* (Loomis, 1942), is listed by Hoffman (1980). He also added that he "by no means [is] assured that *Sinocybe* can be distinguished from *Pseudodesmus*" (Hoffman 1980: p. 117). However, later *Sinocybe* was considered a junior synonym of *Brachycybe* Wood, 1864 (Shelley et al. 2005).

Carl (1912) distinguished the two genera *Platydesmus* and *Pseudodesmus* by the following characters. *Platydesmus* has a collum that is distinctly wider than the head, shaped trapezoidally, with the anterior edge emarginated or notched in the middle; tergite regularly arched, without longitudinal rows of enlarged tubercles; wide ventral sterna, with the coxae of the legs therefore very far apart; and last tergite with tubercles on the apical edge. On the contrary, *Pseudodesmus* has a collum that is not or barely wider than the head, shaped like a crescent or semicircle; tergite more or less distinctly flattened in the middle and with one or more longitudinal rows of enlarged tubercles; the ventral plates very narrow between the insertion of the legs; the coxae therefore are very close together and almost contiguous on the midline of the body; and the last tergite has a smooth apical edge, lacking tubercles.

Up to now, nine species belong to the genus *Pseudodesmus* (in chronological order of descriptions):

1. *Pseudodesmus quadrituberculatus* (Tömösváry 1885) from Matang, Sarawak, Borneo, Malaysia (= *Siphonophora quadrituberculata*: Carl 1912; Jeekel 2001);
2. *Pseudodesmus verrucosus* Pocock, 1887 from Perak, Malay Peninsula, Malaysia (type species of the genus);
3. *Pseudodesmus tuberculatus* (Silvestri 1899) from Peninsular Malaysia;
4. *Pseudodesmus nodulosus* (Verhoeff, 1935) from Sumatra, Indonesia (= *Sumatronium nodulosum*: Hoffman 1980);
5. *Pseudodesmus camptotrichus* (Attems, 1938) from Laos (Bolloven, Paklay, Luong Prabang), Vietnam (Phu Yen: Varella Cap; Khanh Hoa: Hon Ba Mt., Nha Trang; Lam Dong: Lang Biang; Da Nang: Ba Na Mt., Hai Van pass; Kien Giang: Nam Du (Poul Condore); Lao Cai: Sapa); (= *Sumatronium camptotrichum*: Hoffman 1980);
6. *Pseudodesmus variegatus* (Attems, 1938) from Laos (Xieng Khoang) and Vietnam (Lang Bian) (= *Sumatronium variegatum*: Hoffman 1980);
7. *Pseudodesmus leeuweni* (Chamberlin, 1945) from Sibolangir, Sumatra, Indonesia (= *Zinanonium leeuweni*: Hoffman 1980);
8. *Pseudodesmus persimilis* (Attems, 1953) from Laos (Paklay, Luong Prabang) (= *Sumatronium persimile*: Hoffman 1980);
9. *Pseudodesmus kelantanicus* (Sinclair 1901) from the Malay Peninsula (= *Platydesmus kelantanicus*: Carl 1912).

Hoffman (1980), Decker (2014), and Wesener (2015) mentioned 9 species of *Pseudodesmus*, but in MilliBase, there are only 8 species listed (Sierwald et al. 2024). There is some uncertainty regarding a ninth species, but we agree with Carl (1912) who considered *Platydesmus kelantanicus* to be a species of *Pseudodesmus* (Carl 1912). From these, only two species were previously reported from Laos and Vietnam: *Pseudodesmus camptotrichus* and *P. variegatus* (Likhitrakarn et al. 2014). However, *P. persimilis*, originally described from Laos, can probably also occur in Vietnam (Attems 1938, 1953).

This paper is devoted to providing a review of the genus *Pseudodesmus* in Vietnam, descriptions of five new species, and notes on its phylogenetic relationships.

Material and methods

Millipede specimens were collected from various parts of Vietnam during expeditions organized by the Institute of Ecology and Biological Resources (IEBR) and Vietnamese-Russian Tropical Center from 2004 to 2024. Specimens were collected by hand from under logs, rocks, barks, and by pitfall traps. All specimens were preserved in 80% ethanol.

Morphological characters were investigated with an Olympus SZX16 stereomicroscope. Gonopods were dissected for morphological examination and photographed. Colour images were taken at various focal planes using a Sony A6000 camera coupled to a SMZ800N Nikon stereomicroscope. UV images were taken using the aforementioned camera-microscope combination with illumination from a Nichia Convoy UV flashlight. Images were focal stacked using Helicon Focus version 7.0 and assembled in Adobe Photoshop CS6.

Gonopods were removed from the body, preserved in series of increasing ethanol concentrations, 90%, 95% and 99% for dehydration in 24 hours, mounted on an aluminum stuff, then coated with gold. Scanning electron microscope (SEM) images were taken using the Prisma E system (ThermoFisher Scientific) at IEBR.

Total genomic DNA was extracted using a Qiagen DNeasy Blood and Tissue Kit. A 680-bp fragment of the mitochondrial gene, cytochrome c oxidase subunit I (COI), was amplified and sequenced using a pair of universal primers, LCO1490 and HCO2198 (Folmer et al. 1994). Polymerase chain reaction (PCR) conditions for amplification of the COI gene follow those of Nguyen et al. (2017) as follows: an initial denaturation at 95 °C for 2 min followed by 36 cycles of 95 °C for 20 sec, 42 °C for 45 sec, and 72 °C for 1 min, and a final extension at 72 °C for 5 min. The successfully amplified PCR products were submitted to First-Base Company (Malaysia) for purification and sequencing. COI sequences were checked and confirmed using a BLASTN 2.6.0+ search (Zhang et al. 2000) and registered for GenBank with unique accession numbers. All confirmed sequences were aligned using multiple sequence alignment with the program ClustalX ver. 2.0 (Larkin et al. 2007). The

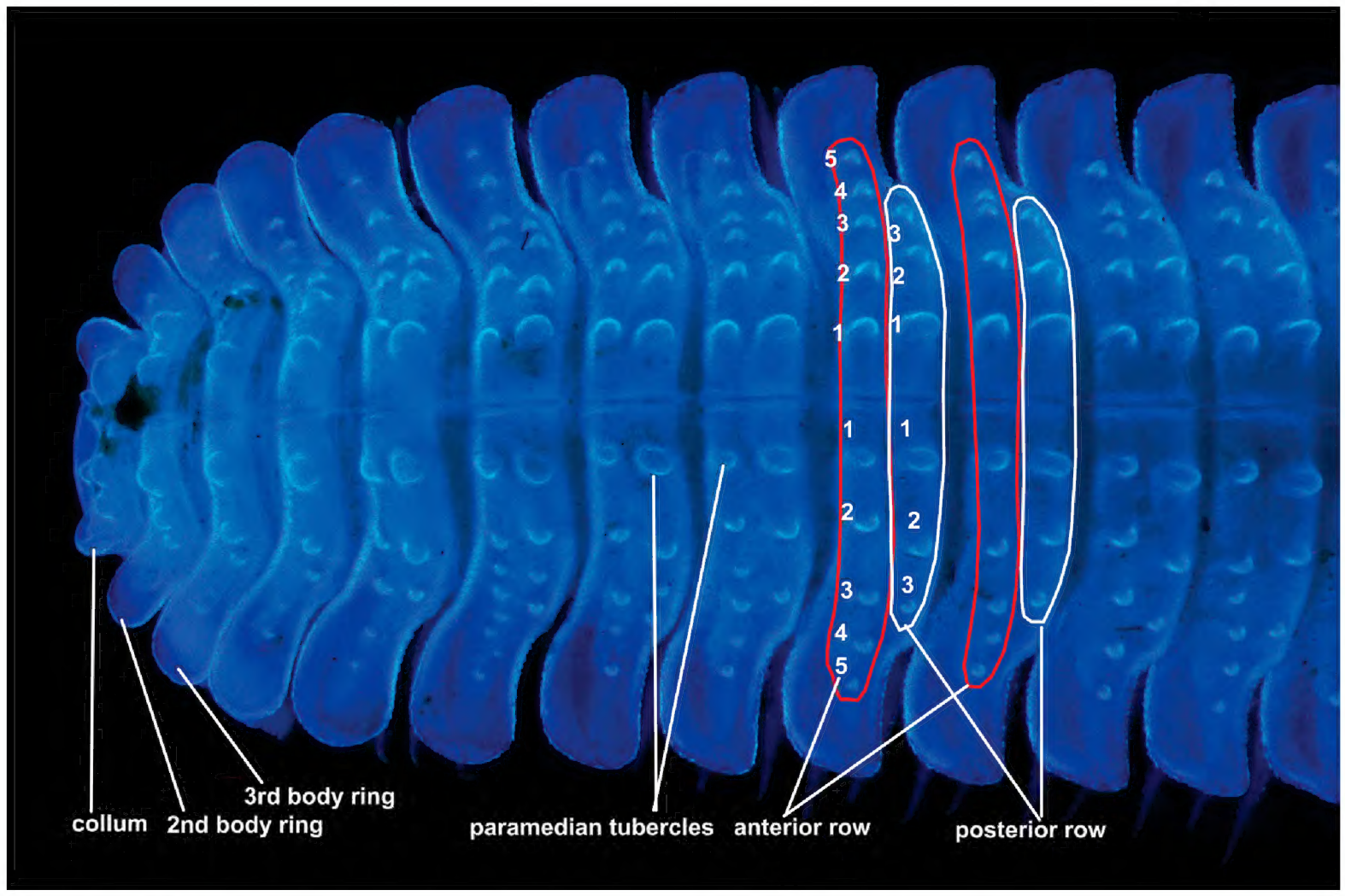

Figure 1. Tubercle notation of *Pseudodesmus bidoup* sp. nov. Numbers refers to tubercles.

genetic distance between platydesmidan samples was calculated using the Kimura 2-parameter model performed in MEGA ver.7.0 (Kumar et al. 2016). A maximum likelihood bootstrap analysis was conducted using the IQTREE server with 1,000 replicates at http://iqtree.cibiv.univie.ac.at/ (Trifinopoulos et al. 2016).

All terminology follows (Mikhaljova et al. 2010). Tubercle notation is shown in Fig. 1. Holotype and paratypes are deposited in IEBR, Hanoi, Vietnam; some are shared with the Department of Zoology, Hungarian Natural History Museum, Budapest, Hungary (HNHM).

Abbreviations

IEBR-Myr = Institute of Ecology and Biological Resources, Myriapod collection; HNHM = Hungarian Natural History Museum, Department of Zoology; NHMW = Naturhistorisches Museum Wien; NP = National Park.

Results

Taxonomy

Order Platydesmida de Saussure, 1860
Family Andrognathidae Cope, 1869
Subfamily Bazillozoniinae Verhoeff, 1935

Genus *Pseudodesmus* Pocock, 1887

Type-species. *Pseudodesmus verrucosus* Pocock, 1887, by original designation. Known only from two female specimens from Perak State, Peninsular Malaysia.

Historical diagnosis. Translated from Latin in Pocock (1887): *Platydesmus* form. With a long body, bearing a series of tubercles above and keels below on each side. With a number of segments numbering greater than seventy; the last segment posteriorly not sharp; the segments, except for the first and last, bearing keels near the lower part of the side, rising close to level, and with a groove along the middle of the back. Each keel, except the first three, has a repugnatorial pore on the lateral margin. The first four segments have two legs each, the others are equipped with two pairs of legs; the last (and possibly the penultimate) lacking legs. The legs consist of six joints; the last joint of the leg is armed with a claw at the tip. The leg-bearing plates are free. The head is bent under the anterior segments, with a convex front; the anterior margin scarcely produced into a snout. Without eyes. Antennae consist of seven articles; located on the sides of the head; the last article being the smallest. The mandibles are hidden. The gnathochilarium is prominent; with large stipes; the jaws and cardines are not conspicuous; there are no lobes on the small, thin lamellae linguales; the mentum is hammer-shaped and large.

According to Wesener (2015), the genus can be recognized by the following characters: “Colour variable. Trunk wide, paraterga strongly elongated. Body length up to 60 mm, with 66–76 body rings. Collum with tubercles. Tergites densely pilose, strongly sculptured, with several smaller and one row of larger tubercles. Larger tubercles sometimes forming a ridge or resembling conic spines”.

Remarks. The genus has been found only in Southeast Asia, but has been poorly studied. Since the description of its last species, *Pseudodesmus persimilis* (Attems, 1953), there has been very little taxonomic information about the genus.

Pseudodesmus camptotrichus (Attems, 1938)

Sumatronium camptotrichum Attems, 1938: p. 303, figs 219–235.

Type material. 26 specimens, including 1 male and 16 females (NHMW-MY2288–2293).

Historical diagnosis. According to Attems (1938, p. 303), the species can be recognized by coloration of earth brown; length 14 mm, width 2 mm, male with 37–42 body rings, female with 35–49 body rings; head almost evenly rounded; collum relatively short, lateral paraterga rounded, anteriad-directed. Metazonites with two rows of 5+5 or 5+4 tubercles on body ring 2, 6–9+6–9 tubercles on the following body rings; the paramedian tubercles the largest, rather elongated.

Records from Vietnam. Khanh Hoa Province (Ba Ngoi; Hon Ba; Po Nagar; Cau Da), Phu Yen Province (Varella), Da Nang Province (Ba Na; Hai Van), Lam Dong Province (Lang Biang), Binh Phuoc Province (Bu Dap), Ba Ria-Vung Tau Province (Con Son isl.) (Attems 1938)(Attems 1938).

Pseudodesmus variegatus (Attems, 1938)

Sumatronium variegatum Attems, 1938: 308, figs 236–243.

Type material. 1 male and 2 juveniles (NHMW-MY2287).

Historical diagnosis. According to Attems (1938: p. 308), the species can be recognized by striking coloration of fairly irregular distribution of black and yellow-brown color; male with 53–56 body rings, length 32 mm, width 5.8 mm; collum scarcely wider than the head; other metazonites densely covered with tiny hairs dorsally on the tubercles and on the underside of paraterga, with 2 transverse rows of shiny tubercles; anterior row of 8–15 + 8–15 tubercles, extending to paraterga; posterior row of 5–7 + 5–7 tubercles present only on metaterga.

Record from Vietnam. Lam Dong Province (Lang Bian).

New species

Pseudodesmus bidoup sp. nov.

https://zoobank.org/0E9D217B-0ED9-41E8-9712-960188EF700A

Figs 2–5

Type material. ***Holotype.*** Vietnam • 1 male; Lam Dong Province, Bi Doup–Nui Ba National Park; 12.11231°N, 108.6627°E; 1,500–1,800 m a.s.l.; 29 April–9 May 2009; Anh D. Nguyen leg; mixed forest; IEBR-Myr 957H.

Paratypes. Vietnam • 1 female, 1 juvenile; same data as for the holotype; IEBR-Myr 957P • 1 female; same data as for the holotype; HNHM • 1 male (41 body rings); Kon Tum Province, Lo Xo pass; 15.23439°N, 107.73386°E; 830 m a.s.l.; 15–19 April 2004; Anh D. Nguyen leg.; secondary forest; pitfall trap; IEBR-Myr 961.

Diagnosis. Head slightly smaller than collum. Collum with two rows of tubercles 1+1(2) smaller and 2+2 larger tubercles. Body smooth, neither setose nor pubescent, midbody rings with two rows of tubercles on metazonites, anterior row longer, extending to about midlength of paraterga, containing 5+5 tubercles; posterior row shorter and extending to base of paraterga, consisting of 3+3 tubercles. Posterior gonopods 6-segmented, distally carrying four apical stylets.

Diagnosis remark. The new species is easily distinguished from *P. camptotrichus* by coloration in alcohol (light yellowish vs earth brown). It also differs from two previously known species, *P. variegatus* and *P. camptotrichus* in having smaller size (number of male body rings: 35 vs 53–56 and 37–42; length: 9.25 mm vs 32 mm and 14 mm; width: 1.63 mm vs 5.8 mm and 2.0 mm, respectively), number of metazonal tubercles (two rows of 5+5 and 3+3 vs two rows of 8–15+8–15 and 5–7+5–7, and two rows of 6+6 to 9+9 each row, respectively).

Description. Male holotype.

Measurements: 35 body rings plus telson; length about 9.25 mm, length of metazona about 0.19 mm, width of metazona about 1.63 mm, width of prozona about 1.25 mm; ratio of width of head and width of collum = 0.93.

Coloration of ethanol-preserved specimen: whole body including legs and antenna light yellowish.

Head almost smooth, not setose, round-shaped. Antenna stout, clavate, *in situ* extending to body ring 4; antennomere 6 > 5 >3 > 4 = 2 > 7=1 in length. Collum with distinct, but small paraterga directed anterolaterad (Figs 2B, 3A); two rows of tubercles on collum: anterior row with 1+1 small tubercles, posterior row with 2+2 large tubercles including larger paramedian ones (Fig. 3A). Body smooth, neither setose nor pubescent. Metatergites elevated medially and slightly declined laterad, so body in cross-section subtriangular. Terga 2–4 with a row of 2–4+2–4 large tubercles including 2+2 tubercles on paraterga (Figs 2B, 3A); other terga with two rows of tubercles, anterior row longer, extending to about midlength of paraterga, containing 5+5 tubercles; posterior row shorter and extending to base of paraterga, consisting of 3–4+3–4 tubercles. Paramedian tubercles considerably larger (Figs 2A–C, 3A, B).

Paraterga slightly curved anteriad on body rings 2–5, lateral margins rounded (Fig. 2A, B); increasingly less so curved the following body rings, slightly curved caudad on body rings 25–27, and strongly curved caudad on body rings 28–31; caudal corners of paraterga increasingly acute on 6–7 posteriormost body rings in front of telson; paraterga of penultimate body ring produced strongly caudad and flanking telson (Figs 2A–C, 3A, B). All margins of paraterga serrated, with tiny setae.

Telson (Figs 2C, 3D) short, caudal margin rounded; epiproct with 2+2 small/tiny tubercles at caudal margin. Paraprocts and hypoproct semi-circular.

Legs slender, shorter than mid-metazonal width, terminating before lateral margins of paraterga. Prefemur = tarsus > femur > postfemur = tibia in length. Claws normal. Coxal sacs present from body rings 3–28 (Fig. 3D).

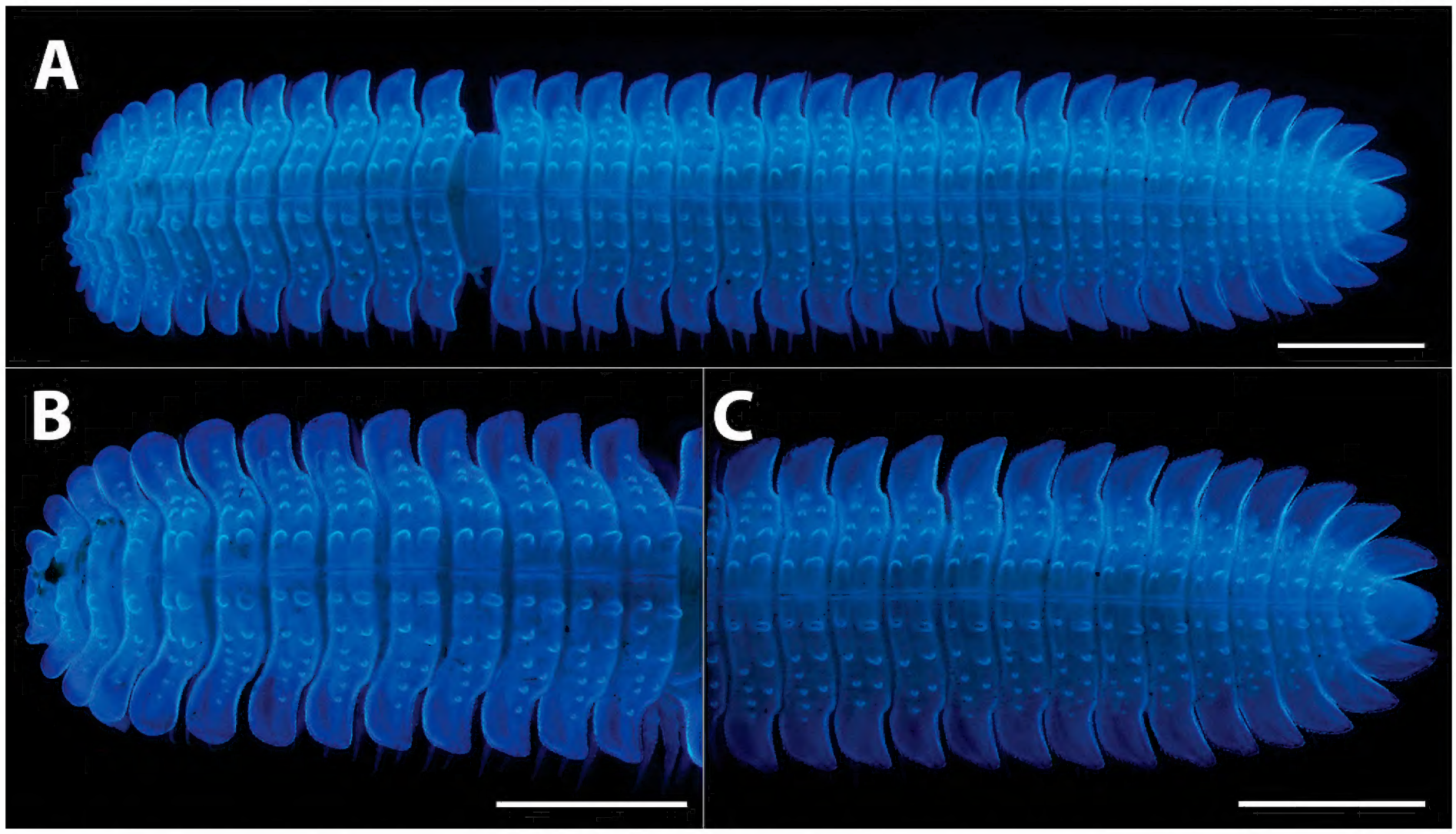

Figure 2. *Pseudodesmus bidoup* sp. nov. Holotype (IEBR-Myr 957), under UV light. **A.** Habitus, dorsal view; **B.** Anterior part of body, dorsal view; **C.** Posterior part of body, dorsal view. Scale bars: 1 mm.

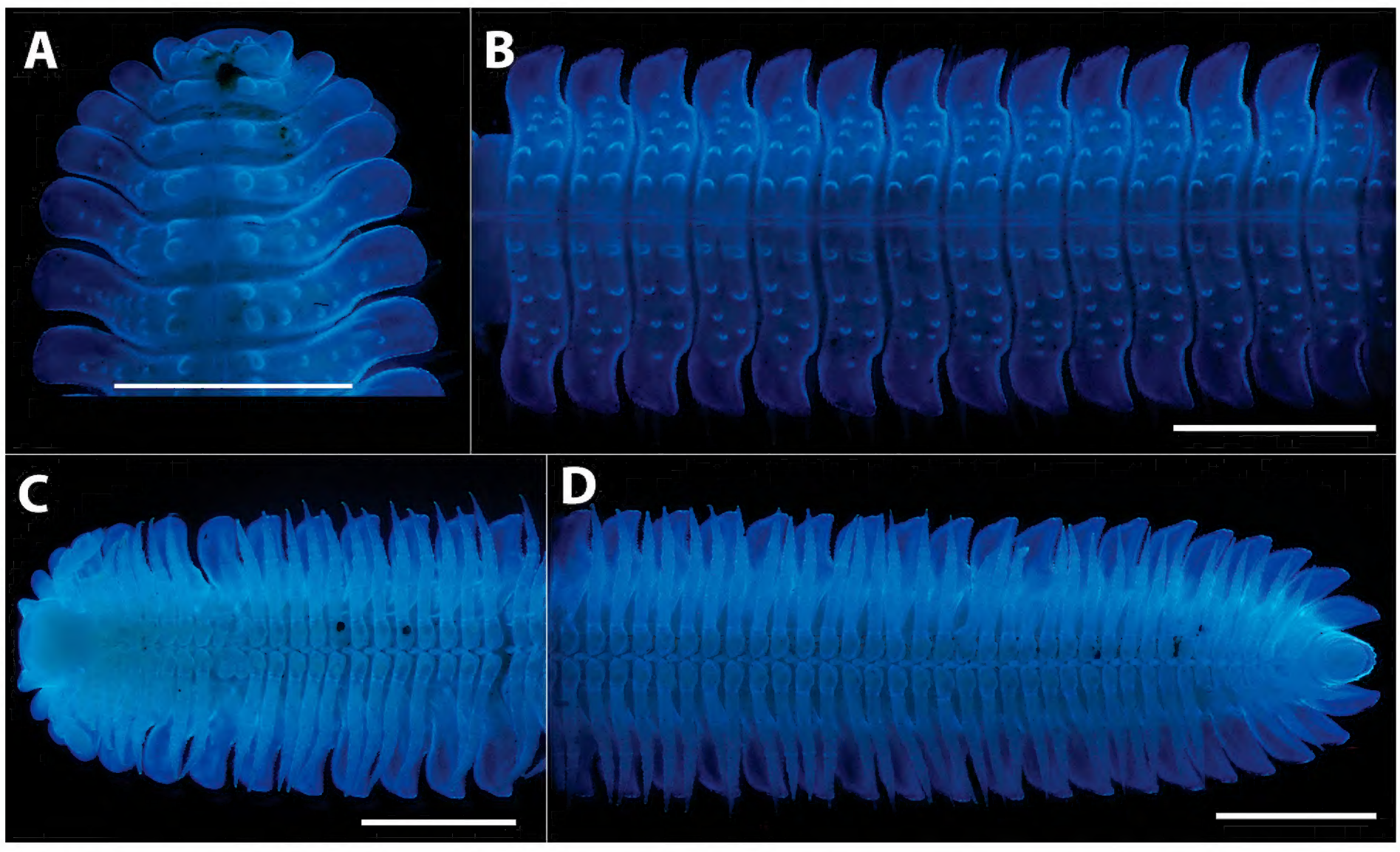

Figure 3. *Pseudodesmus bidoup* sp. nov. Holotype (IEBR-Myr 957), under UV light. **A.** Collum and body rings 2–6, dorsal view; **B.** Midbody body rings, dorsal view; **C.** Anterior part of body, ventral view; **D.** Posterior part of body, ventral view. Scale bars: 1 mm.

Gonopods: Two pairs of gonopods directed anteromesad. Anterior gonopods (Figs 4A, 5A, B) 6-segmented, covered with long setae; coxite broad, basal part sparsely covered with microgranulations; podomere 3 and ultimate podomere (*po6*) longest; ultimate podomere with distal long, thick setae (*mse*). Posterior gonopods (Figs 3B, 4C, D) 6-segmented, covered with sparse long setae; coxite broadly large, basal part sparsely covered with microgranulations; podomeres 2–5 short and stout, somewhat equal in length; ultimate podomere (*po6*) longest, with four apical stylets (*sty*).

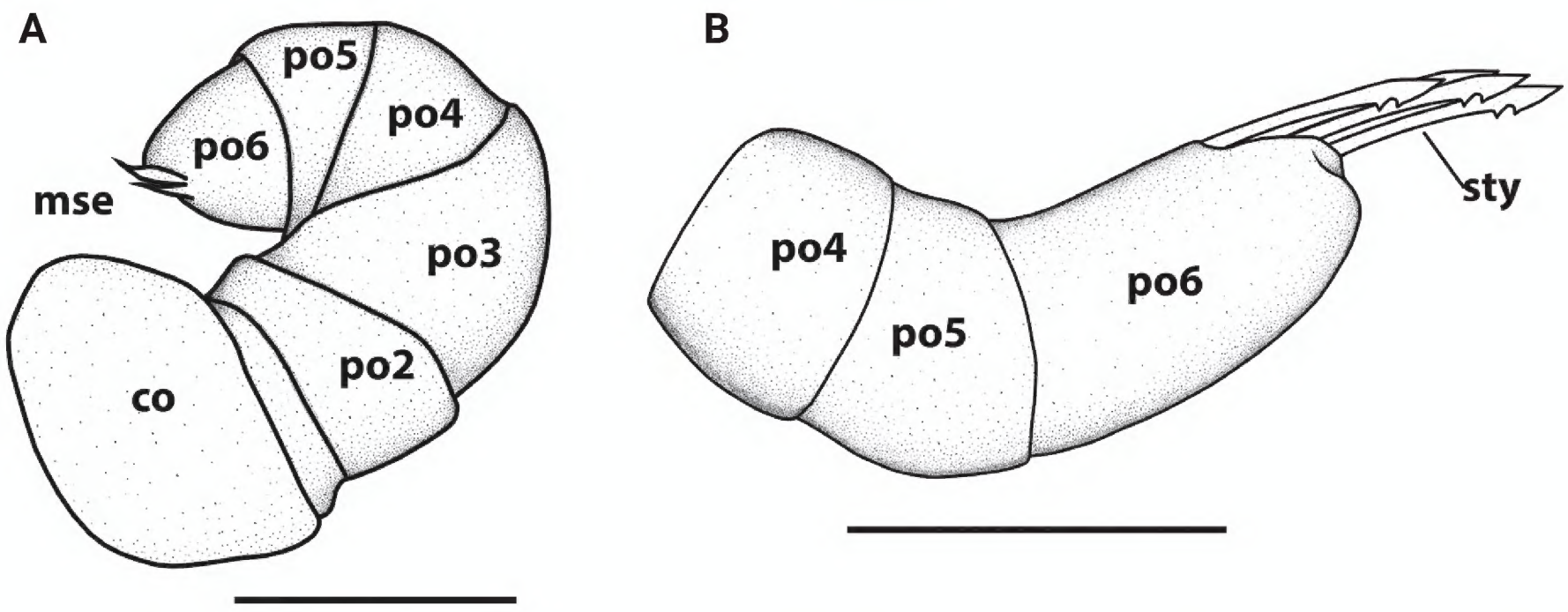

Figure 4. *Pseudodesmus bidoup* sp. nov. Holotype (IEBR-Myr 957). Gonopods. **A.** Right anterior gonopods, anterior view; **B.** Right posterior gonopod, distal part, ventral view. *Abbreviations*: co = coxite = podomere 1; po2 = podomere 2; po3 = podomere 3; po4 = podomere 4; po5 = podomere 5; po6 = podomere 6 (ultimate podomere); mse = macrosetae; sty = stylet. Scale bars: 0.1 mm.

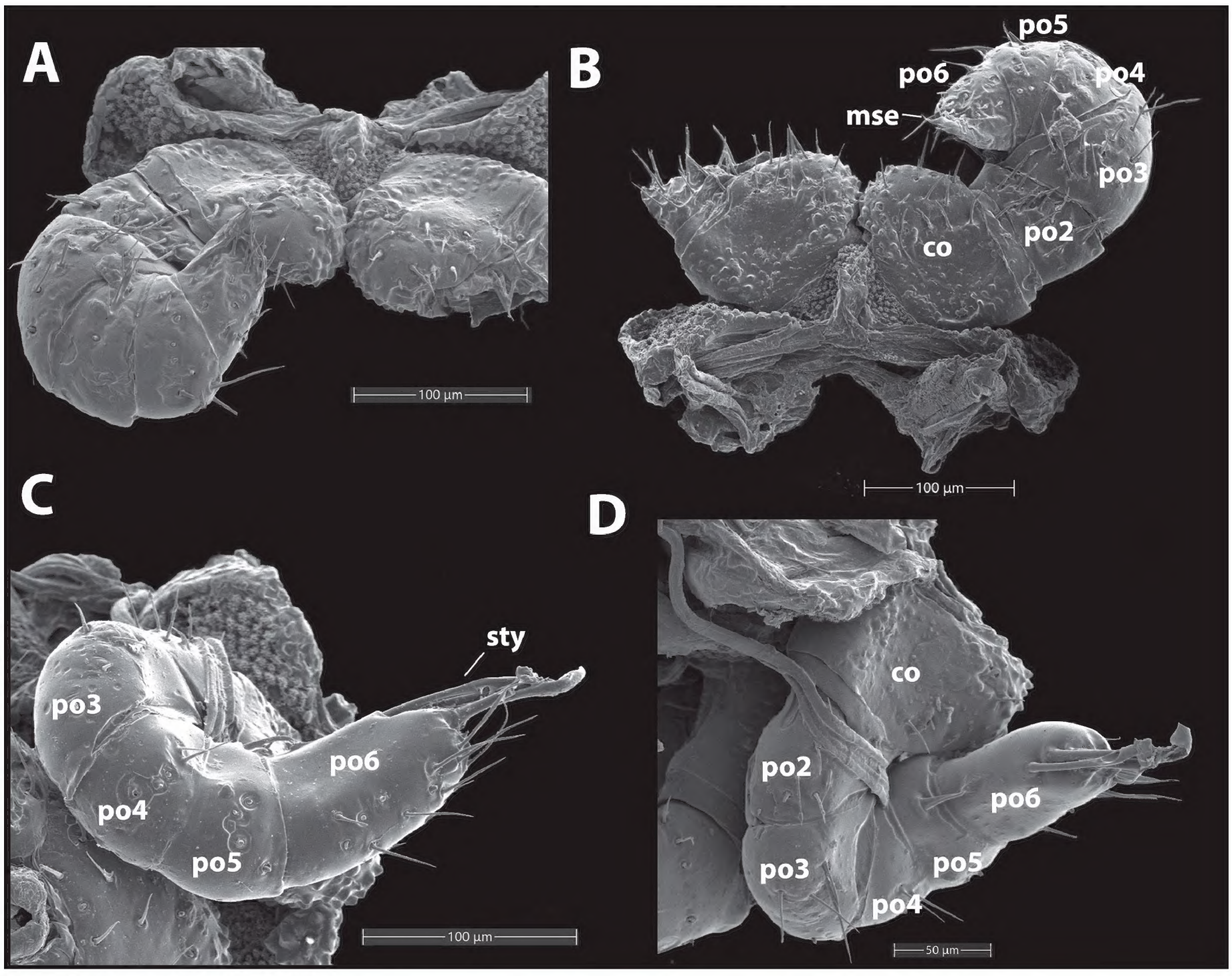

Figure 5. *Pseudodesmus bidoup* sp. nov. Holotype (IEBR-Myr 957). Gonopods. SEM. **A, B.** Right anterior gonopods, ventral view (**A**), anterior view (**B**); **C, D.** Right posterior gonopod, ventral view (**C**), sublateral view (**D**). *Abbreviations*: co = coxite = podomere 1; po2 = podomere 2; po3 = podomere 3; po4 = podomere 4; po5 = podomere 5; po6 = podomere 6 (ultimate podomere); mse = macrosetae; sty = stylet.

Variation. ***Female paratype:*** number of body rings 43–44 plus telson, length ca. 13.75–14.50 mm, length of midbody metazonites about 0.27–0.31 mm, width of midbody metazonite and prozonite ca. 2.25–2.50 mm and 1.56–1.63 mm, respectively; ratio of width of head and width of collum = 0.96. Nonsexual characters as in male.

The male sample IEBR-Myr 961 has strong tubercles, even on the collum, then on every body ring the two (1+1) median posterior tubercles form a strong paramedian crest along the entire body. Anterior tubercles are also the same but smaller. Color is uniformly yellowish, without a dark pattern.

Etymology. Named after the "Bi Doup" mountain, type locality. Noun in apposition.

Distribution. The species has been found in mixed forests and regenerated forests in Kon Tum and Lam Dong provinces, Highlands of Vietnam.

DNA barcoding. Sequencing a fragment of the COI gene failed.

Pseudodesmus ngoclinh sp. nov.

https://zoobank.org/3132C8AB-185A-4282-873E-274B50C0ECC7

Figs 6–10

Material examined. ***Holotype.*** Vietnam • 1 male; Kon Tum Province, Ngoc Linh Mts; 15.07134°N, 107.97158°E; 1,800–1,900 m a.s.l.; 21 Mar.–9 Apr. 2006; Anh D. Nguyen leg.; primary forest, decaying wood, under the bark; IEBR-Myr 986H.

Paratypes. Vietnam • 1 male, 2 females; same data as for the holotype; IEBR-Myr 986P • 2 females; same data as for the holotype; HNHM.

Diagnosis. Head slightly broader than collum. Collum with distinct paraterga directed anterad, with two rows of 1+1 smaller and 2+2 larger tubercles. Body covered with dense minute pubescence. Midbody body rings with two rows of tubercles on metazona, posterior row of 4–5+4–5 tubercles, shorter and extending to base of paraterga; anterior row of 5–10 + 5–10 small tubercles, longer, extending to about midlength of paraterga. Posterior gonopods 6-segmented, with two apical stylets.

Diagnosis remarks. The new species is easily distinguished from *P. camptotrichus* by coloration (yellowish/brownish plus dark spots vs whole earth brown). It also differs from *P. variegatus* and *P. camptotrichus* in having smaller size (length: 11.4 mm vs 32 mm and 14 mm; width: 2.74 mm vs 5.8 mm and 2.0 mm, respestively), number of metazonal tubercles (two rows of 5–10 + 5–10 and 4–5+4–5 vs two rows of 8–15+8–15 and 5–7+5–7, and two rows of 6+6 to 9+9 each row, respectively).

Description. Male holotype.

Measurements: 51 body rings plus telson; length about 11.40 mm, length of midbody metazona about 0.19 mm, width of midbody metazona about 2.74 mm, width of midbody prozona about 1.26 mm; ratio of width of head and width of collum = 1.05.

Coloration of ethanol-preserved specimens: first 6 body rings including collum yellowish in the middle, then most body rings with a light median section, dark spots (on tubercles) irregularly on one side or both sides, dark spots on paraterga, asymmetrically, and almost every body ring different, sometimes repeating 3–4 body rings, last 5–6 body rings uniformly brownish.

Head (Figs 6A, B, F, 7A–D) round-shaped, moderately densely setose. Antenna stout, clavate, *in situ* reaching to body ring 5; antennomere 6 > 5 >3 > 4 = 2 > 7 = 1 in length. Collum with distinct paraterga directed anterad, with two rows: anterior row with 1+1 tubercles, posterior row with 2+2 tubercles, paramedian ones being larger (Figs 6A, 7A, B). Body covered with dense minute pubescence. Slopes of dorsum steep, so body in cross-section subtriangular. Body rings 2–4 with a single row, each of 1+2, 1+1, 3+4 tubercles, respectively (Figs 6A, C, 7A). Midbody body rings with two rows of tubercles on metazona, posterior row of 4–5+4–5 tubercles, shorter and extending to base of paraterga; anterior row of 5–10 + 5–10 small tubercles, longer, extending to about midlength of paraterga. Paramedian tubercles considerably larger, and posterior paramedian tubercles much larger than anterior paramedian ones (Figs 6D, 8A, 8C). The last 6 body rings with only a row of 4+4 tubercles (Figs 6E, 8C).

Paraterga curved strongly anteriad on body rings 2–5, increasingly less so on body rings 6–10 (to body ring 11 on paratype specimens), slightly curved caudad on body ring 11 (to body ring 12 on paratype specimens) and following body rings; caudal curvature of paraterga increasingly clear on 6–7 posteriormost body rings in front of telson; paraterga of penultimate body ring produced strictly caudad and flanking telson (Figs 6E, G, 8C, D). Caudal paratergal margins entire, without notches (Figs 6–8).

Telson (Figs 6C, 8C, D) short, caudal margin rounded; epiproct with 2+2 small/tiny tubercles at caudal margin. Paraprocts and hypoproct semi-circular.

Legs slender, shorter than width of body ring together with paraterga, terminating before lateral paratergal margins. Prefemur = tarsus > femur > postfemur = tibia in length. Claws normal. Coxal sacs present on body rings 3–41 (Figs 6G, 8B).

Gonopods: Two pairs of gonopods directed mesoanteriad. Anterior gonopods (Figs 9A, 10A, B) 6-segmented, covered with long setae; coxite broadly stout, basal part sparsely covered with microgranulations; podomeres 2–5, short and stout; podomere 6 slightly longer than other podomeres, distally carrying macrosetae (*mse*). Posterior gonopods (Figs 9B, 10C, D) 6-segmented, covered with sparse long setae; coxite broad, basal part sparsely covered with microgranulations; podomeres 2–5 short and stout; ultimate podomere (*po6*) longest, with two apical stylets (*sty*).

Variation. ***Male paratype:*** 53 body rings + telson; length about 11.73 mm, length of midbody metazona about 0.21 mm, width of midbody metazona about 2.79 mm, width of midbody prozona about 1.28 mm.

Female paratypes. 48–51 body rings + telson. Length *ca* 12.21–13.52 mm, width of midbody metazona about 2.84–3.02 mm; width of prozona about 1.32 mm; length of metazona about 0.26 mm, average ratio of width of head and width of collum = 1.14. Nonsexual characters as in male.

Etymology. Named after the "Ngoc Linh" Mountain, the type locality. Noun in apposition.

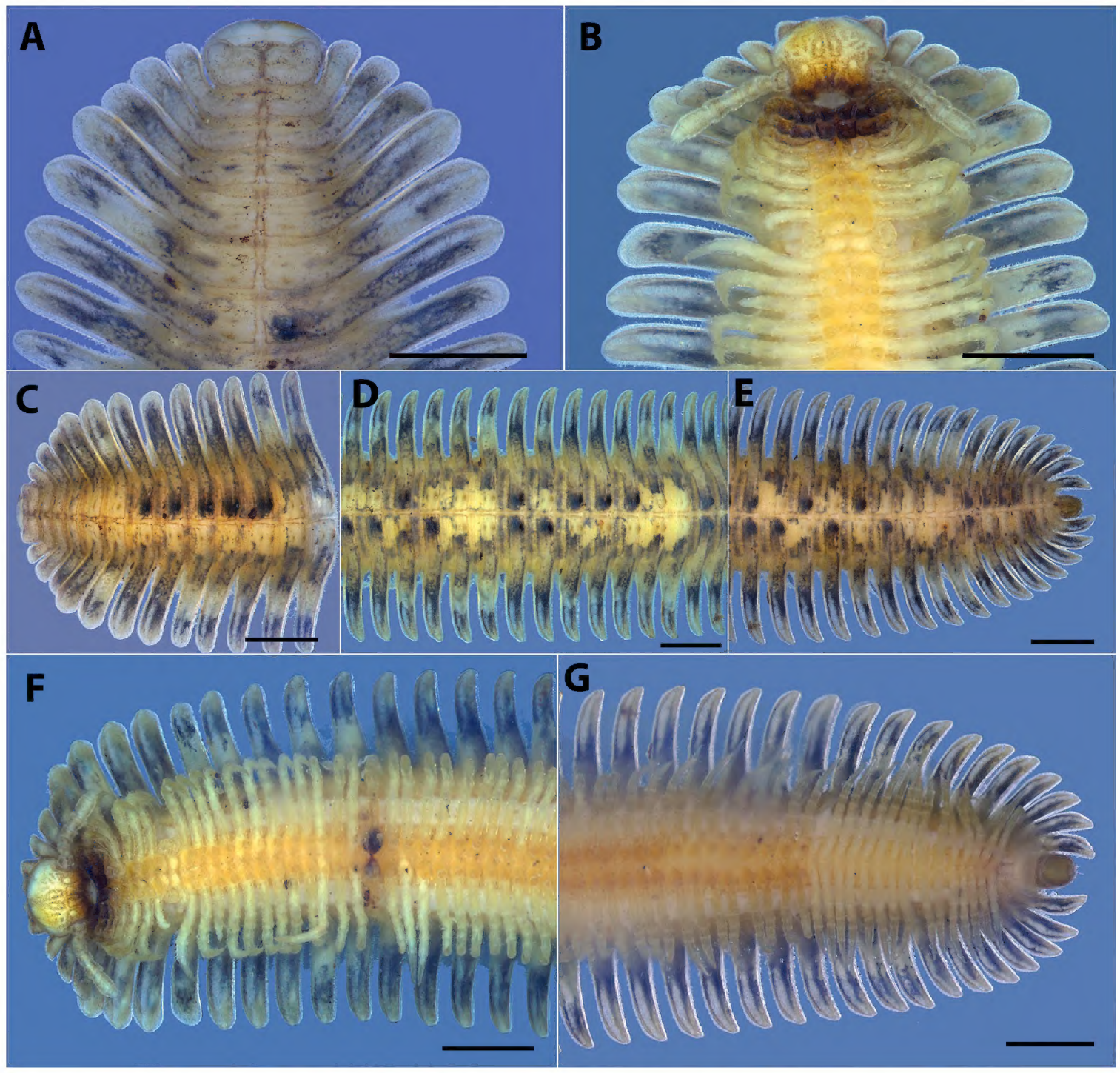

Figure 6. *Pseudodesmus ngoclinh* sp. nov, holotype (IEBR-Myr 986H), under white light. **A–C.** Anterior part of body, dorsal view (**A, C**), ventral view (**B**); **D.** Midbody body rings, ventral view; **E.** Posterior part of body dorsal view; **F.** Anterior half of body, ventral view; **G.** Posterior half of body, ventral view. Scale bars: 1 mm.

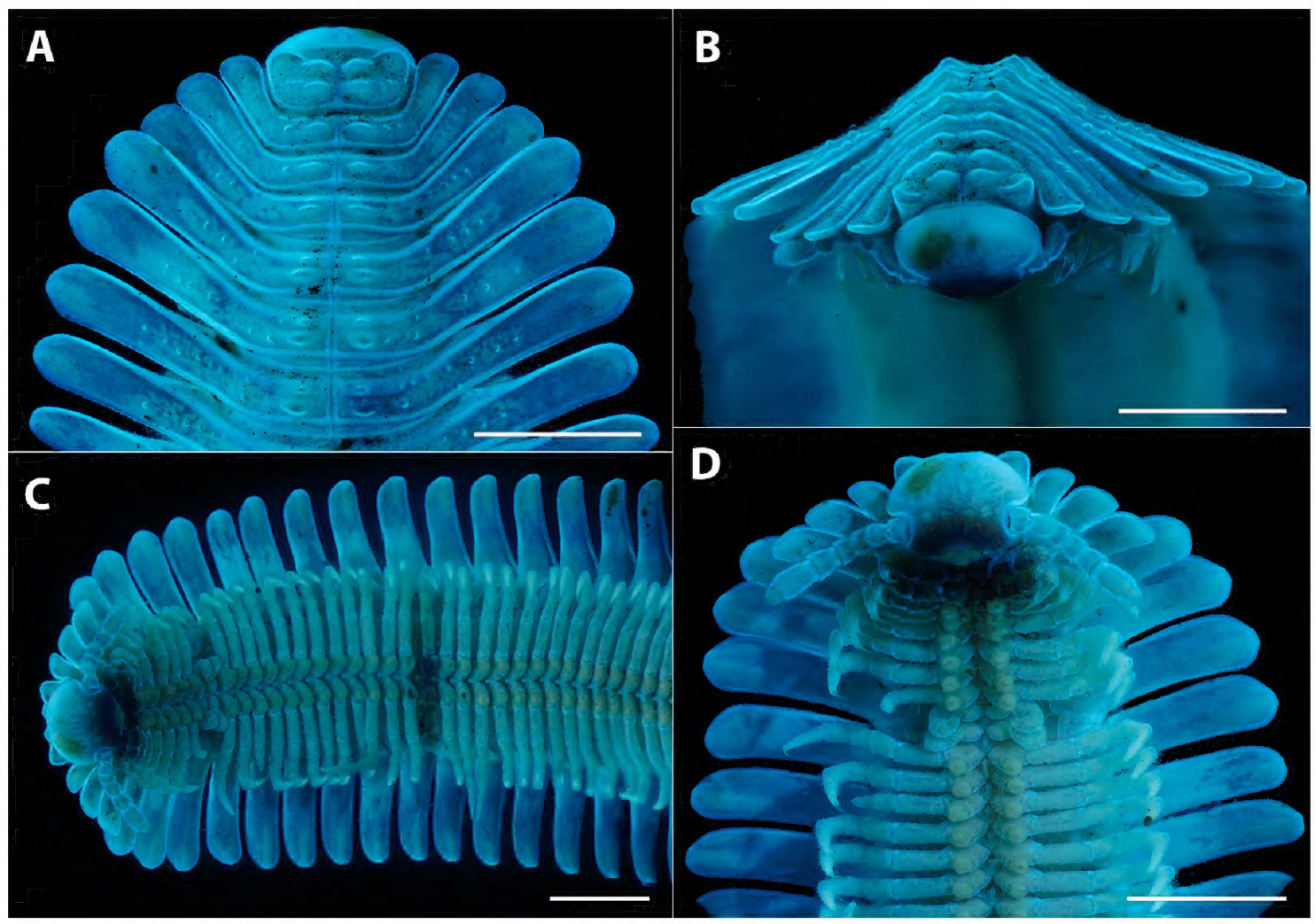

Figure 7. *Pseudodesmus ngoclinh* sp. nov, holotype (IEBR-Myr 986H), under UV light. **A.** Anterior part of body, dorsal view; **B.** Head and collum, anterior view; **C.** Anterior half of body, ventral view; **D.** Anterior part of body, ventral view. Scale bars: 1 mm.

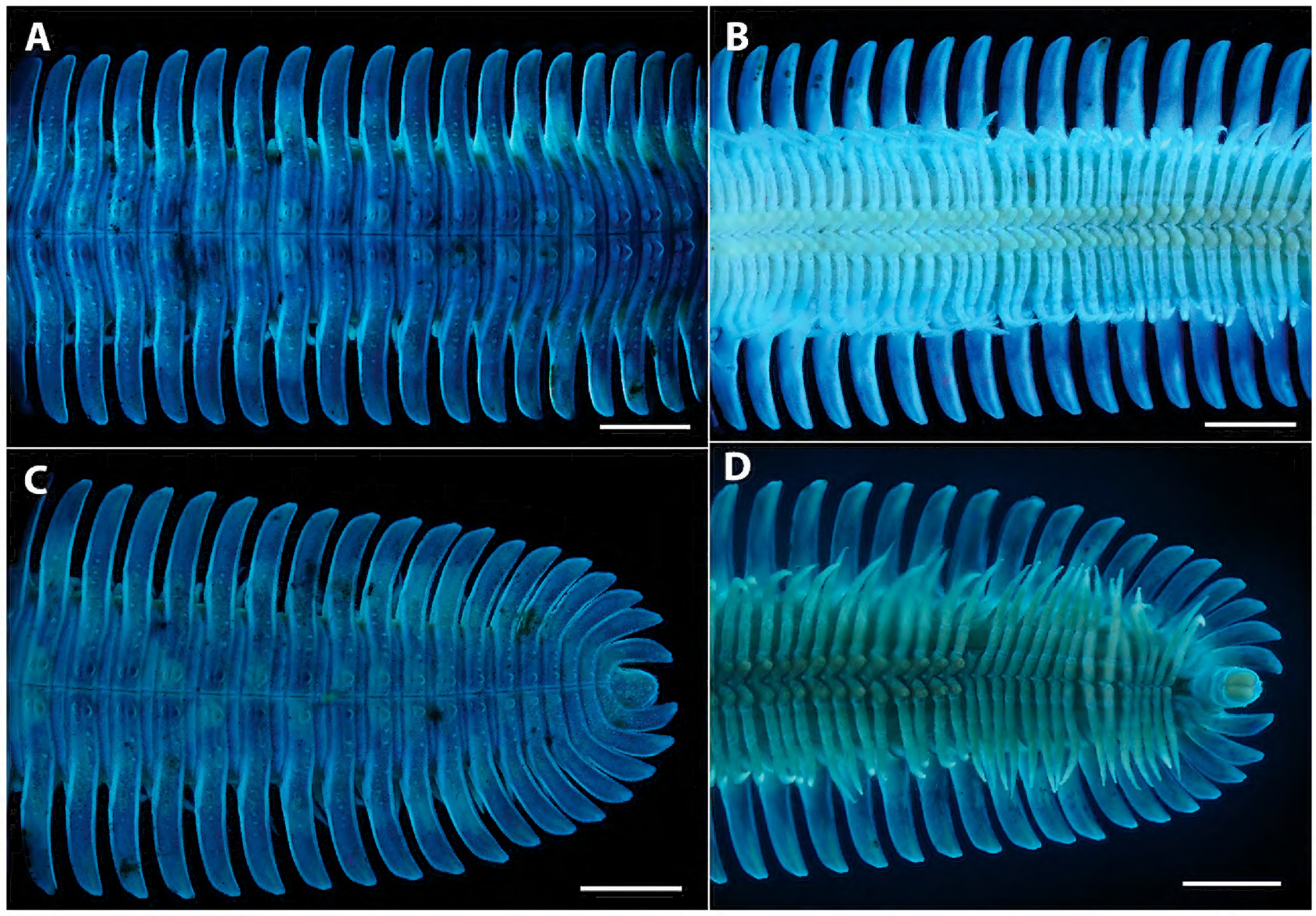

Figure 8. *Pseudodesmus ngoclinh* sp. nov, holotype (IEBR-Myr 986H), under UV light. **A, B.** Midbody body rings, dorsal view (**A**), ventral view (**B**); **C, D.** Posterior half of body, dorsal view (**C**), ventral view (**D**). Scale bars: 1 mm.

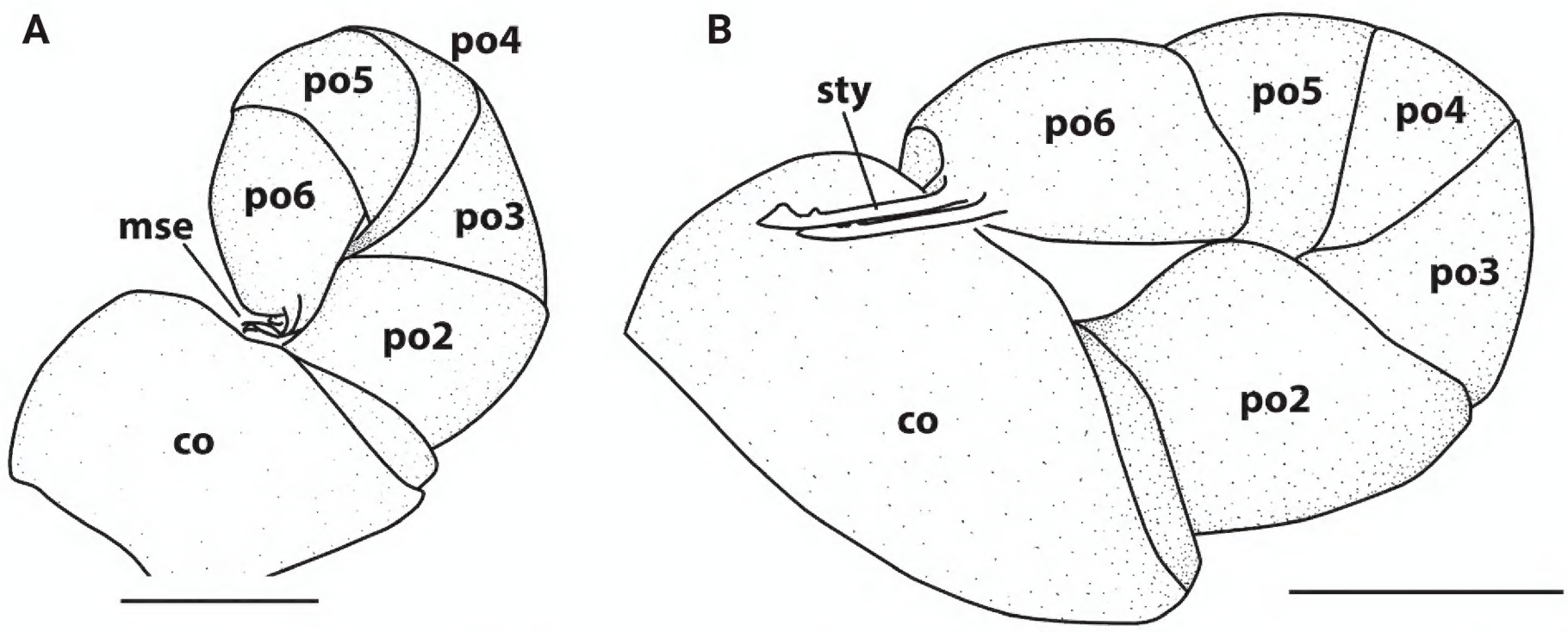

Figure 9. *Pseudodesmus ngoclinh* sp. nov, holotype (IEBR-Myr 986H), gonopods. **A.** Left anterior gonopod, ventral view; **B.** Posterior gonopods, anterior view. *Abbreviations*: co = coxite = podomere 1; po2 = podomere 2; po3 = podomere 3; po4 = podomere 4; po5 = podomere 5; po6 = podomere 6 (ultimate podomere); mse = macrosetae; sty = stylet. Scale bars: 0.1 mm.

Distribution. The species has been found in Ngoc Linh Mts at the high elevation of 1800–1900 m a.s.l. in Kon Tum Province, Vietnam.

DNA barcoding. A fragment of the COI gene is accessioned at NCBI GenBank with the following accession numbers: PQ423222–PQ423223. The new species has a COI gene similarity with Androgna thidae spp. (MF983566 and MF983567) of 89.13% and 89.37% identity, respectively.

Pseudodesmus karstomus sp. nov.

https://zoobank.org/0EE484F0-C29F-439C-B717-5478C9838FEF

Figs 11–14

Material examined. ***Holotype.*** Vietnam • 1 male; Cao Bang Province, Tra Linh District, Quoc Toan commune, Thang Hen Lake, near Ham Huong cave; 22.7588°N, 106.2958°E, 1 Nov. 2021; A.D. Nguyen leg.; IEBR-Myr 959H.

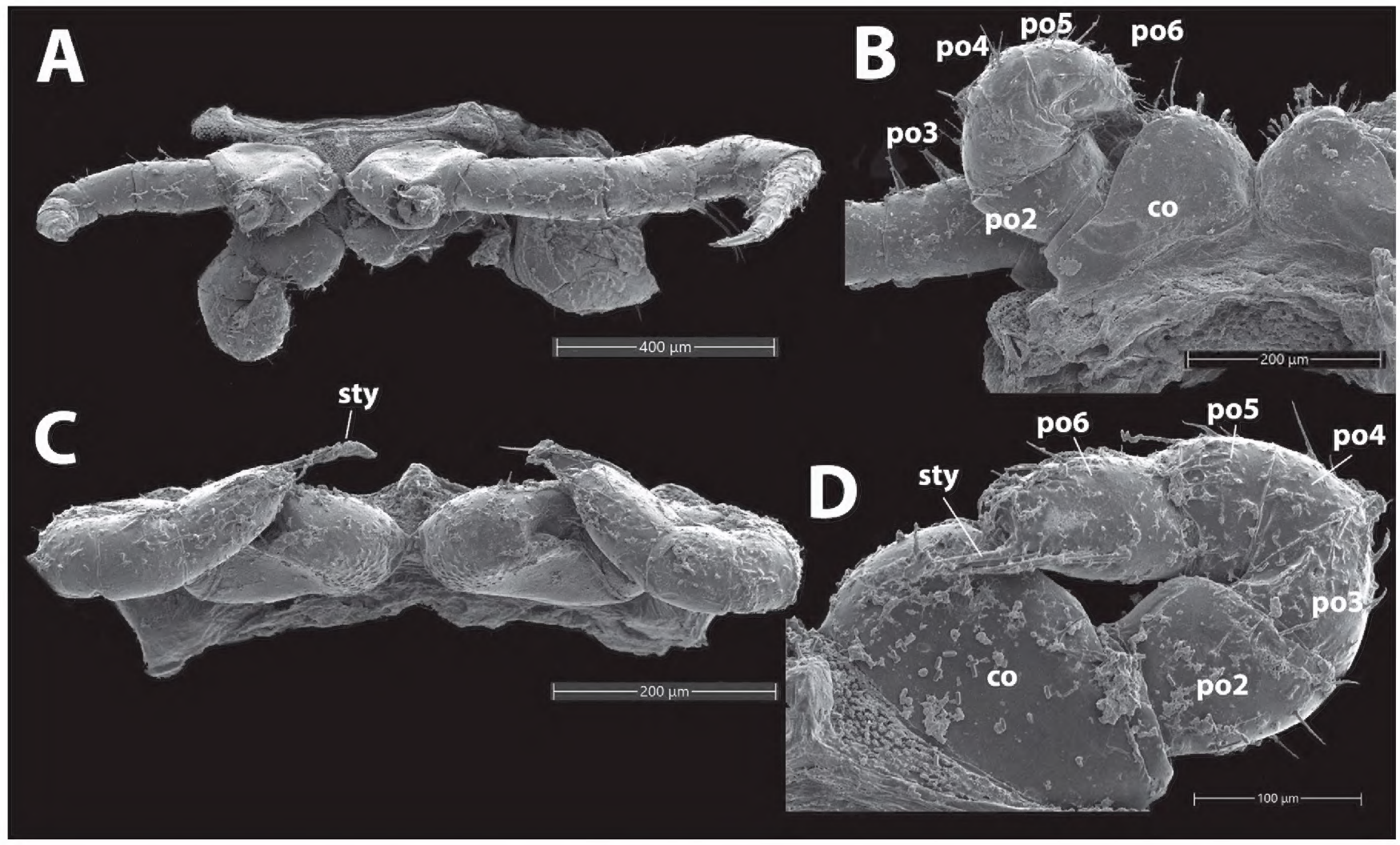

Figure 10. *Pseudodesmus ngoclinh* sp. nov, holotype (IEBR-Myr 986H), gonopods. SEM. **A, B.** Left anterior gonopod, ventral view (**A**), posterior view (**B**); **C, D.** Posterior gonopods, ventral view (**C**), anterior view (**B**). *Abbreviations*: co = coxite = podomere 1; po2 = podomere 2; po3 = podomere 3; po4 = podomere 4; po5 = podomere 5; po6 = podomere 6 (ultimate podomere); mse = macrosetae; sty = stylet.

Paratypes. Vietnam • 1 male, 1 female same data as for the holotype; IEBR-Myr 959P • 1 male; same data as for the holotype; HNHM.

Diagnosis. Terga and base of paraterga marbled yellowish brown with some blackish tubercles on several body rings. Head triangular-shaped, slightly narrower than collum. Collum stout strongly bilobed, anteriorly excavated, with small 2 bumps in the middle, densely setose. Midbody metazonae with two rows of tubercles, anterior row with 7–8+7–8 tubercles, posterior one with 2+2 tubercles. Posterior gonopods 6-segmented, with two apical stylets and two lateroapical stylets.

Diagnosis remarks. The new species is easily distinguished from *P. camptotrichus* by coloration (marbled yellowish brown with some blackish tubercles vs earth brown), larger size (length: 18.64 mm vs 14 mm; width: 2.74 mm vs 2.0 mm), number of metazonal tubercles (two rows of 7–8+7–8 and 2+2 tubercles vs two rows of 6+6 to 9+9 each row).

It also differs from *P. variegatus* in having smaller size (length: 18.64 mm vs 32.0 mm; width: 2.74 mm vs 5.8 mm), number of metazonal tubercles (two rows of 7–8+7–8 and 2+2 tubercles vs two rows of 8–15+8–15 and 5–7+5–7).

Pseudodesmus karstomus sp. nov. is differentiated from two above new species, *P. bidoup* sp.nov. and *P. ngoclinh* sp.nov in body size and number of gonopod stylets. It shares with *P. bidoup* sp.nov. a posterior gonopod with four distal stylets, but two species are distinguished by body size (length: 18.62 mm vs 9.25 mm; width: 4.05 mm vs 1.63 mm). *Pseudodesmus karstomus* is also larger than *P. ngoclinh* (length: 18.62 mm vs 11.4 mm; width: 4.05 mm vs 2.74 mm), and having more distal stylets in posterior gonopod (four vs two).

Description. Male holotype.

Measurements: 61 body rings plus telson, length about 18.64 mm, length of midbody metazona ca. 0.29 mm, width of midbody metazona ca. 4.05 mm, width of midbody prozona ca. 1.35 mm; ratio of width of head and width of collum = 0.98.

Coloration of ethanol-preserved specimens: Terga and base of paraterga marbled yellowish brown with some blackish tubercles on several body rings. Collum and first 4 body rings yellow, 5th weakly brownish, then increasing color pattern: 6–10th light in the middle and brownish at the base of paraterga, 11–12th dark brown in the middle and light borwn at the base of paraterga; then the same pattern repeated as 4 light+3 brown, 5 light+3 brown, 5 light+3 brown, 5 light+3 brown, 3 light+2 brown, 2 light+2 light brown, 3 light in the middle and brownish at the base of paraterga, then the ultimate 3 body rings plus telson and light yellow (Fig. 11A–C). Paraterga paler in preserved specimens, but pinkish in alive specimens.

Head (Figs 11D, E, 12D, E) somewhat smooth, triangular-shaped. Antenna short, somewhat stout, *in situ* extending to body ring 5; antennomere 6 > 5 >3 > 4 = 2 > 7 = 1 in length. Collum (Figs 11D, E, 12D, E) stout strongly bilobed, anteriorly excavated, with two small bumps in the middle, densely setose. Paraterga very tiny, somewhat like lateral keels, caudal margin similar lateral keels.

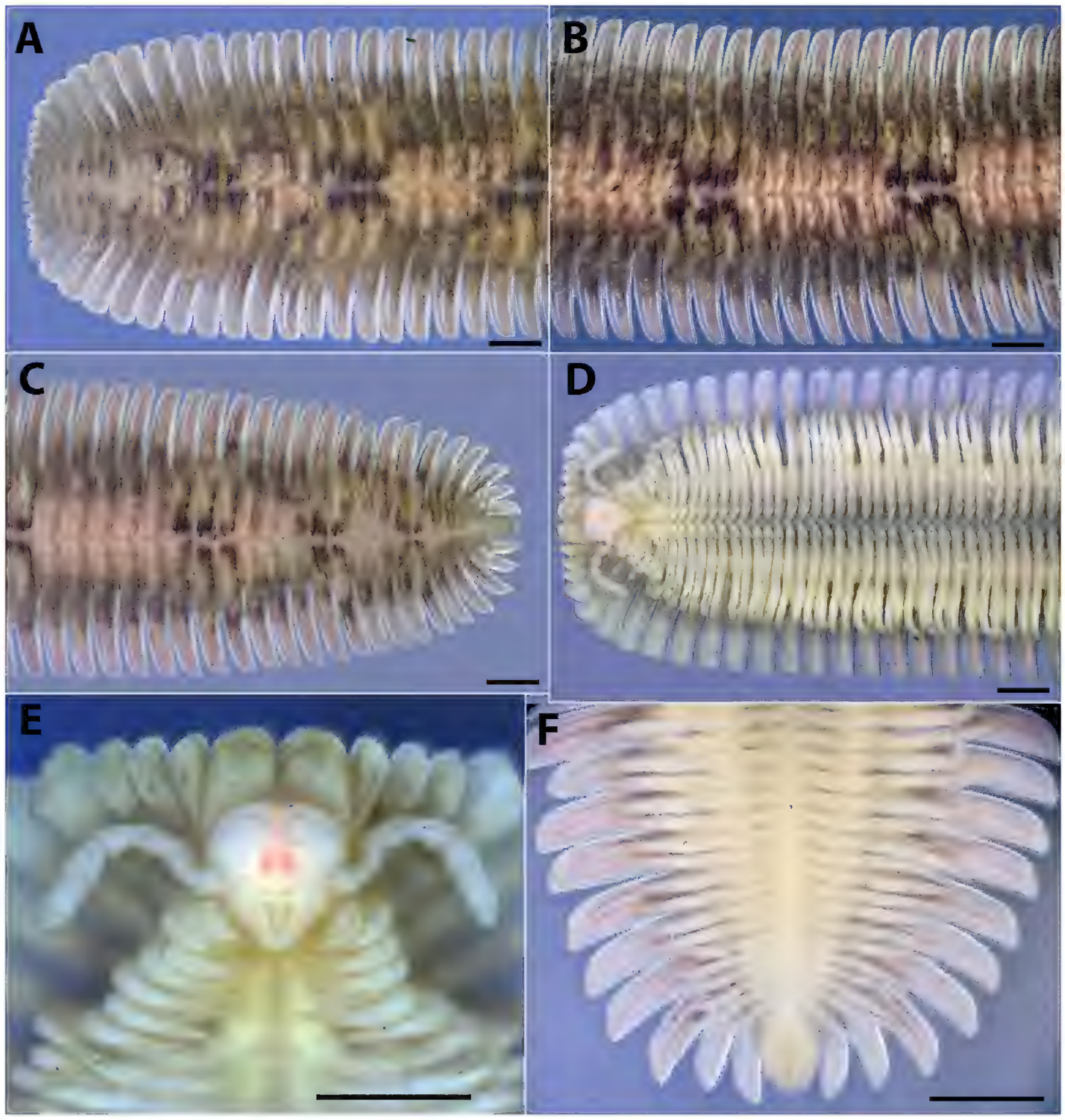

Figure 11. *Pseudodesmus karstomus* sp. nov. Holotype (IEBR-Myr 959H), under white light. **A.** Anterior part of body, dorsal view; **B.** Midbody body rings, dorsal view; **C.** Posterior part of body, dorsal view; **D.** Anterior part of body, ventral view; **E.** Head and collum, ventral view; **F.** Posteriormost part of body, ventral view. Scale bars: 1 mm.

Tergum 2 with a row of 1+1 large, subtriangular tubercles, those tubercles reducing to rather small ones on subsequent terga. Terga 2–5 with one row, from 6th onward with two rows of tubercles, anterior row with 7–8+7–8 tubercles, reaching the middle of paraterga, posterior row with only 2+2, never extending to paraterga; the 1+1 median tubercles (both anterior and posterior) transversally enlarged, elongated, oval (Figs 11A–C, 12A–C).

Paraterga in general very wide (Figs 11, 12). Paraterga 2–3 (Figs 11D, E, 12D, E) anterad directed; paraterga 3–5 extending slightly lateroanterad, paraterga 6–58 laterad, 59–61 lateroposteriad, 62–63 posteriad. Paraterga 1–13 rectangular, from 14th onwards tapering laterad, anterior edge increasingly bending backwards.

Telson (Figs 11C, F, 12C, F) short, caudal margin rounded; epiproct with 3+3 setiferous tubercles at caudal margin (Figs 11C, F, 12C, F). Paraproct and hypoproct semi-circular (Figs 11F, 12F).

Legs slender, shorter than paraterga, terminating before lateral paratergal margins. Claws normal. Coxal sacs present ventrally on body rings 3–59 (Figs 11F, 12F).

Gonopods (Figs 13, 14): Two pairs of gonopods directed mesoanteriad. Anterior gonopods (Figs 13A, 14A, B, F) 6-segmented, covered with long setae; coxite (*co*) broad, basal part sparsely covered with microgranulations; podomeres 2–5, short and stout; podomere 6 slightly longer than other podomeres, distally carrying macrosetae (*mse*). Posterior gonopods (Figs 13B, 14C, D, E) 6-segmented, covered with sparse long setae; coxite (*co*) broad, basal part sparsely covered with microgranulations; podomeres 2–5 short and stout; ultimate podomere (*po6*) longest, with two apical stylets and two lateroapical stylets (*sty*).

Variation. ***Male paratypes*** have 62–63 plus telson, length about 17.76–17.92 mm, length of midbody metazoan ca. 0.29–0.33 mm, width of midbody metazona ca. 2.90–2.94 mm, width of midbody prozona ca. 1.37–1.45 mm; average ratio of width of head and width of collum = 0.89 (width of collum: 0.61 mm, width of head: 0.68 mm).

Female paratype. 66 body rings plus telson; length about 22.36 mm, length of midbody metazoan ca. 0.42 mm, width of midbody metazona ca. 4.06 mm, width

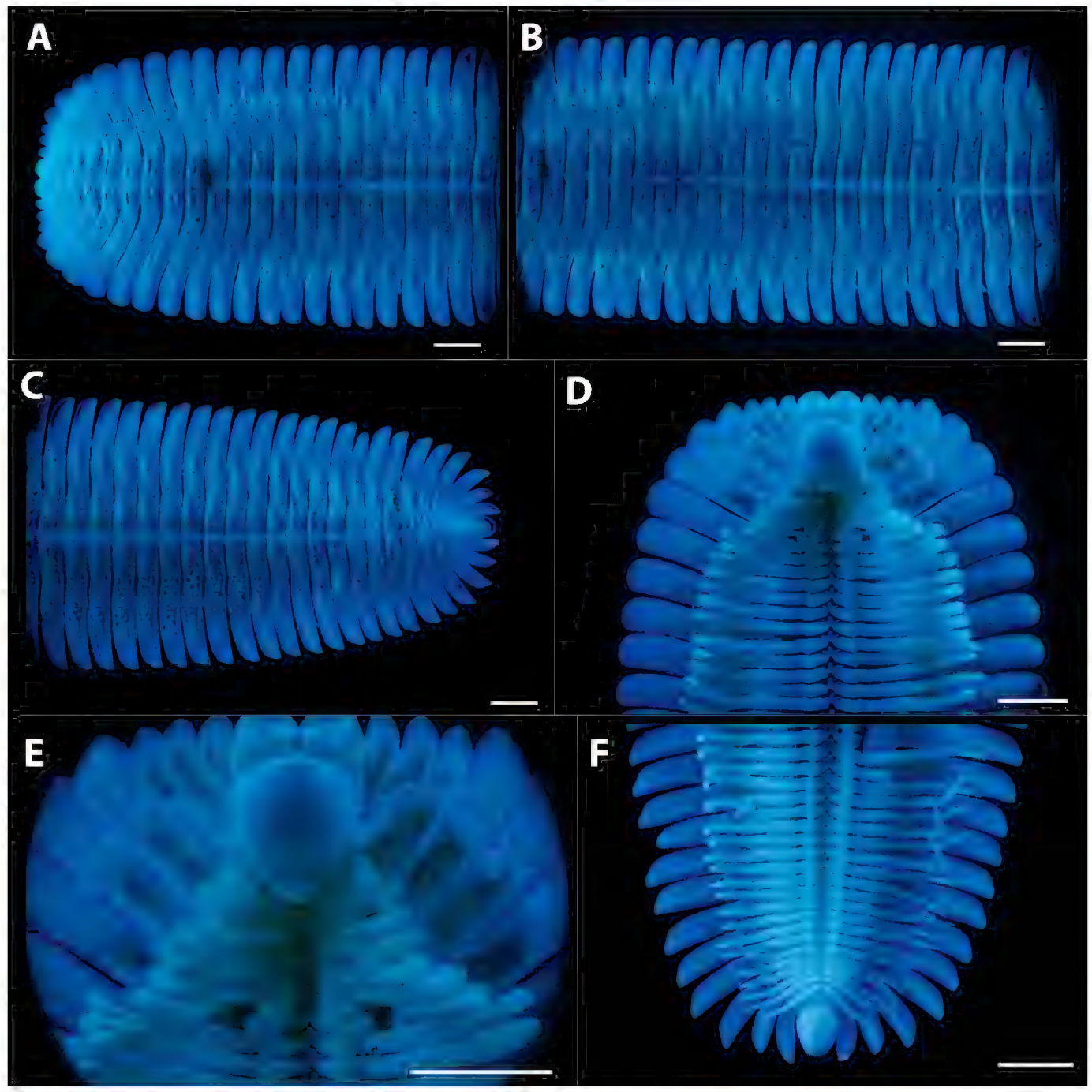

Figure 12. *Pseudodesmus karstomus* sp. nov. Holotype (IEBR-Myr 959H), under UV light. **A.** Anterior part of body, dorsal view; **B.** Midbody body rings, dorsal view; **C.** Posterior part of body, dorsal view; **D.** Anterior part of body, ventral view; **E.** Head and collum, ventral view; **F.** Posterior part of body, ventral vie. Scale bars: 1 mm.

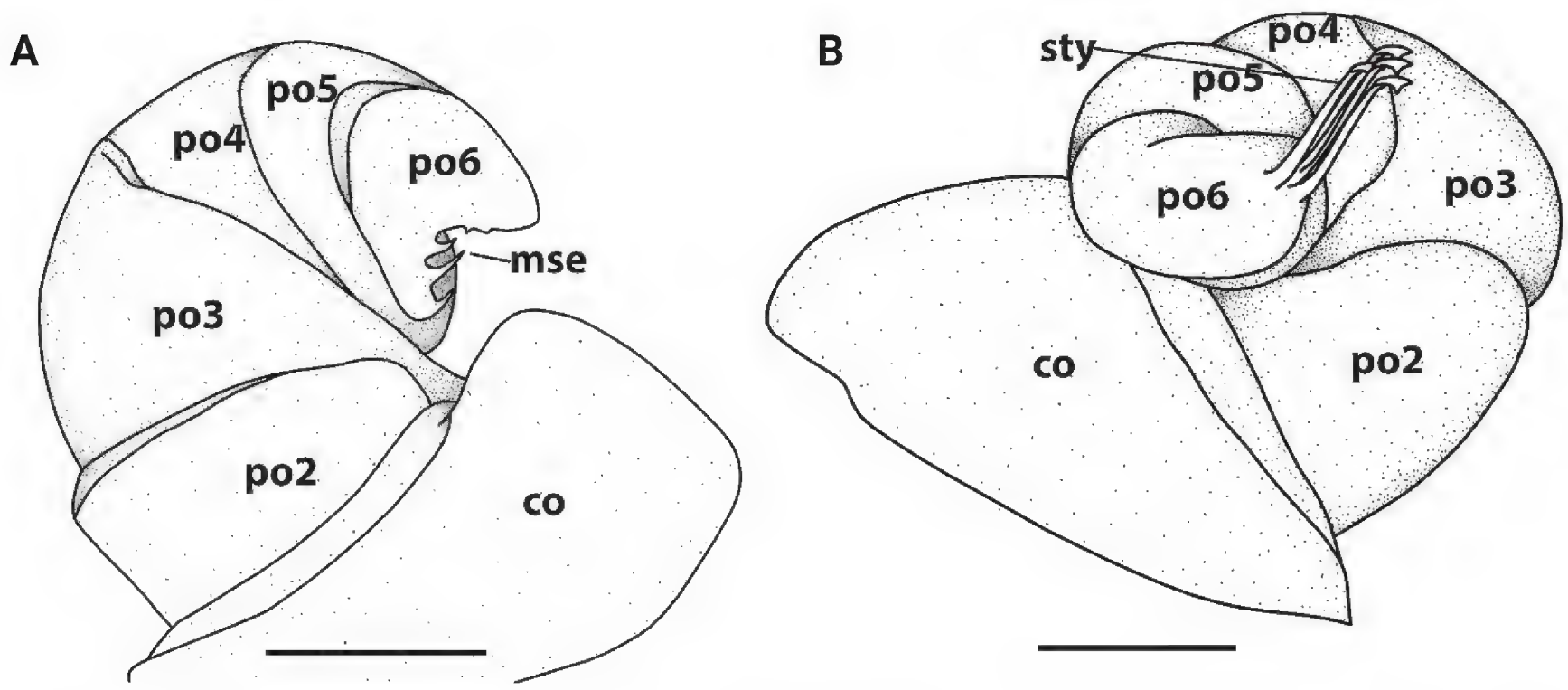

Figure 13. *Pseudodesmus karstomus* sp. nov. Holotype (IEBR-Myr 959H), gonopods. **A.** Left anterior gonopods, anterior view. **B.** Right posterior gonopods, anterior view. *Abbreviations*: co = coxite = podomere 1; po2 = podomere 2; po3 = podomere 3; po4 = podomere 4; po5 = podomere 5; po6 = podomere 6 (ultimate podomere); mse = macrosetae; sty = stylet. Scale bars: 0.1 mm.

of midbody prozona ca. 1.75 mm; ratio of width of head and width of collum = 0.9 (width of collum: 0.72 mm, width of head: 0.65 mm). Nonsexual characters as in male.

Etymology. Named to emphasize the type locality, karst areas. Noun in apposition.

Distribution. The species was found in limestone mountain in Cao Bang Province, northern Vietnam.

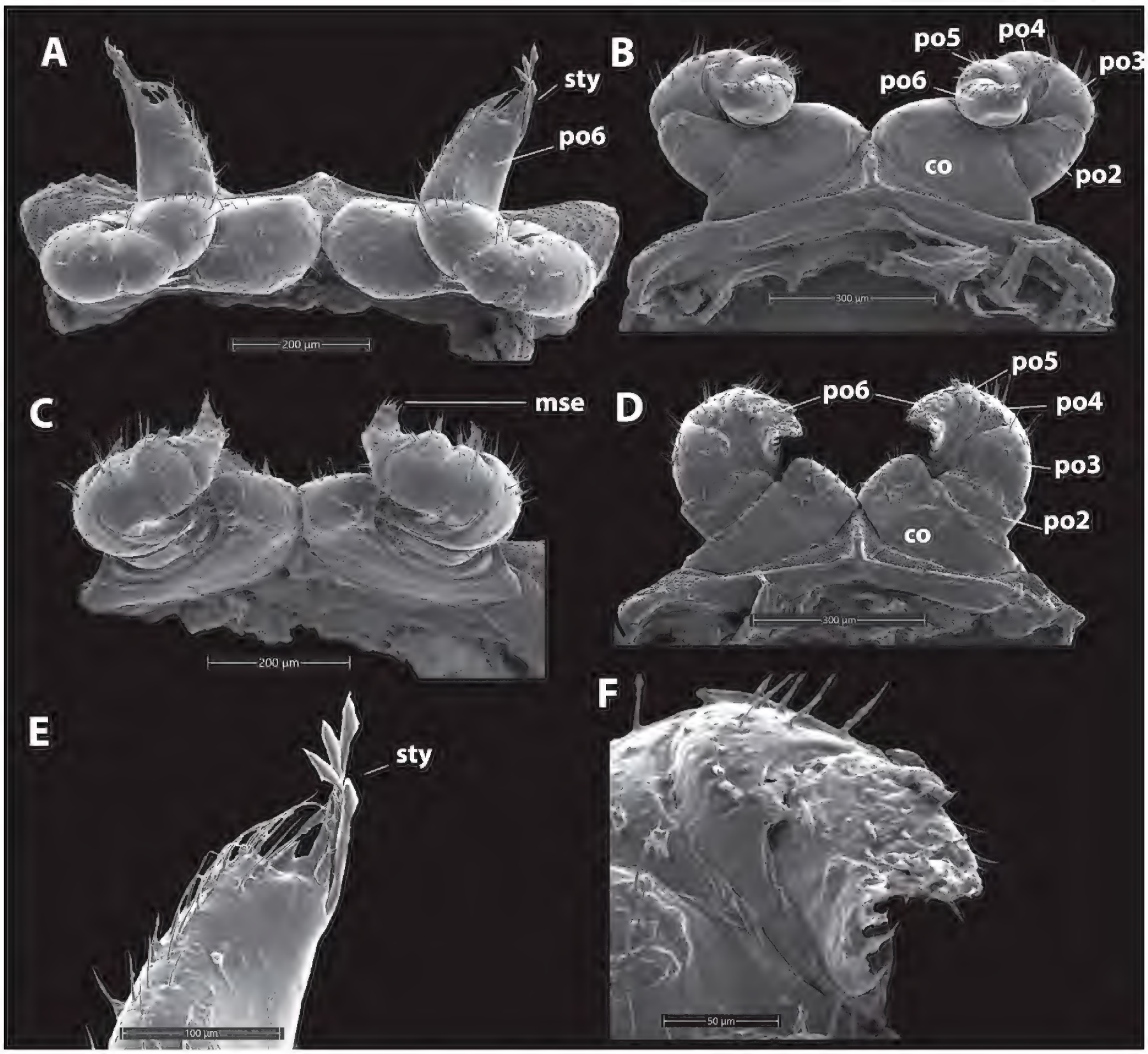

Figure 14. *Pseudodesmus karstomus* sp. nov. Holotype (IEBR-Myr 959H), gonopods. SEM. **A, B.** Posterior gonopods, ventral view (**A**), anterior view (**B**); **C, D.** Anterior gonopods, ventral view (**C**), anterior view (**D**); **E.** Apical stylets of posterior gonopod, ventral view; **F.** Distal part of anterior gonopod, anterior view. *Abbreviations*: co = coxite = podomere 1; po2 = podomere 2; po3 = podomere 3; po4 = podomere 4; po5 = podomere 5; po6 = podomere 6 (ultimate podomere); mse = macrosetae; sty = stylet.

DNA barcoding. A fragment of the COI gene is accessioned at NCBI GenBank with the following accession numbers: PQ423224–PQ423225. The new species has a close COI gene similarity with *Gosodesmus claremontus* (JX962723) of 85.14% in the BLAST search.

Pseudodesmus condao sp. nov.

https://zoobank.org/CE1AD5B1-0A85-447A-91FF-1B490A38097D

Figs 15–20

Material examined. ***Holotype.*** Vietnam • 1 male; Ba Ria-Vung Tau Province, Con Dao NP, on the way to Ong Dung Beach; 08.70528°N, 106.59158°E, 37 m a.s.l., 7 Nov. 2019; A.D. Nguyen leg.; natural forest; IEBR-Myr 982H.

Paratypes. Vietnam • 2 males, 2 females; same data as the holotype; IEBR-Myr 982P • 3 males, 1 female Ba Ria-Vung Tau Province, Con Dao NP, on the way to Ong Dung beach, 08.70528°N, 106.59158°E, 37 m a.s.l., 7 November 2019, leg. Nguyen A.D.; natural forest; IEBR Myr 821 • 8 males, 5 females; Ba Ria-Vung Tau Province, Con Dao NP, on the way to Ong Dung beach, 08.70528°N, 106.59158°E, 37 m a.s.l.; 8 Nov. 2023; A.D. Nguyen leg.; natural forest; IEBR-Myr 977 • 2 males, 2 females; same data as for sample IEBR-Myr 977; HNHM.

Diagnosis. Color dark yellow, little darker in the middle. Head distinctly smaller than collum. Collum bilobed, each with three anterior lobes, no tubercles. Midbody terga with two rows, 3–4 + 3–4 large and 4– 5 + 4– 5 large tubercles in anterior and posterior rows, respectively. Posterior gonopods 6-segmented, with two apical stylets.

Diagnosis remarks. The new species is very similar with *P. camptotrichus* by coloration (dark yellow vs earth brown), but it differs from *P. variegatus* in body coloration (dark yellow vs yellow-brown with black spots).

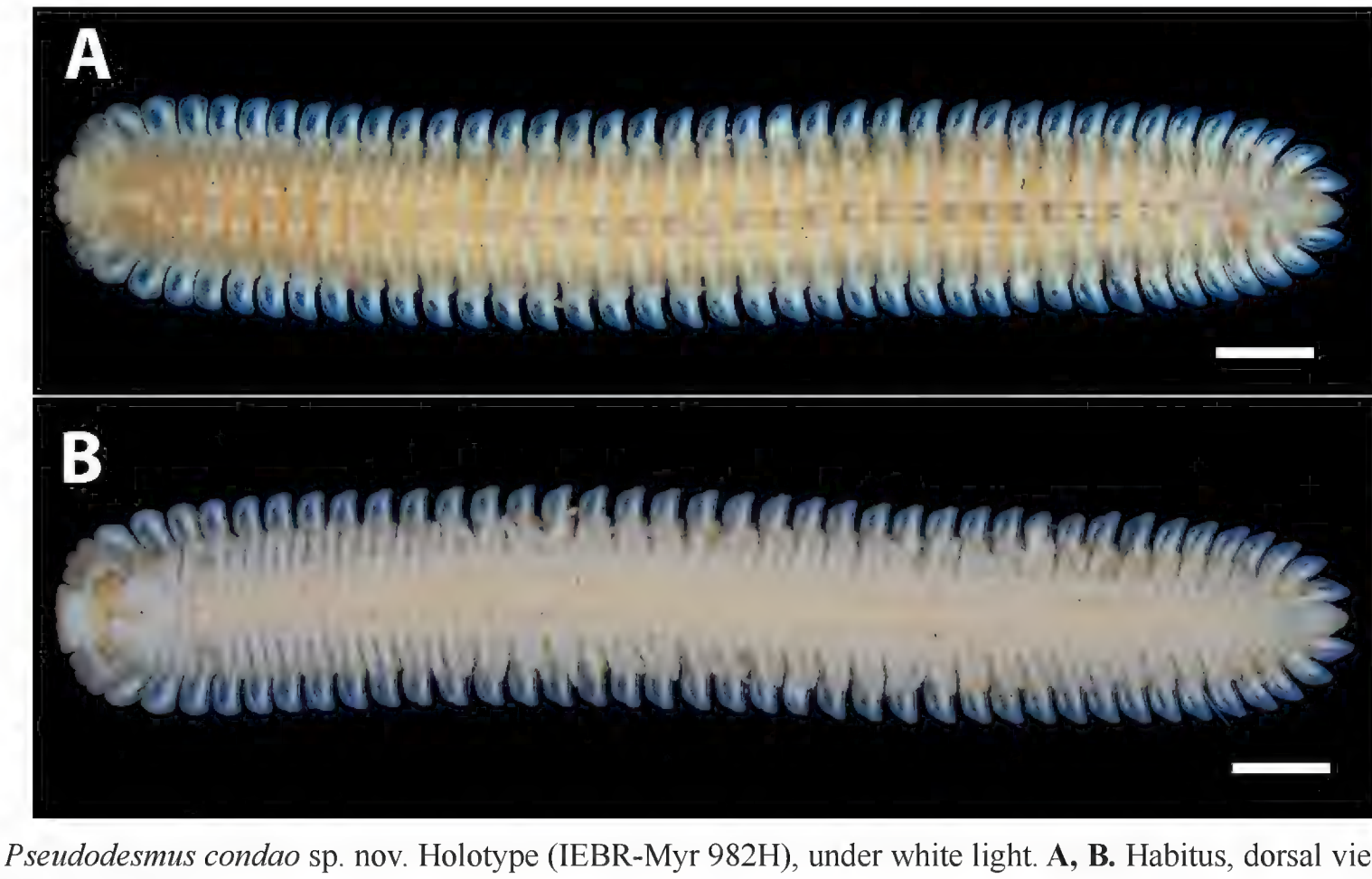

Figure 15. *Pseudodesmus condao* sp. nov. Holotype (IEBR-Myr 982H), under white light. **A, B.** Habitus, dorsal view (**A**), ventral view (**B**). Scale bars: 1 mm.

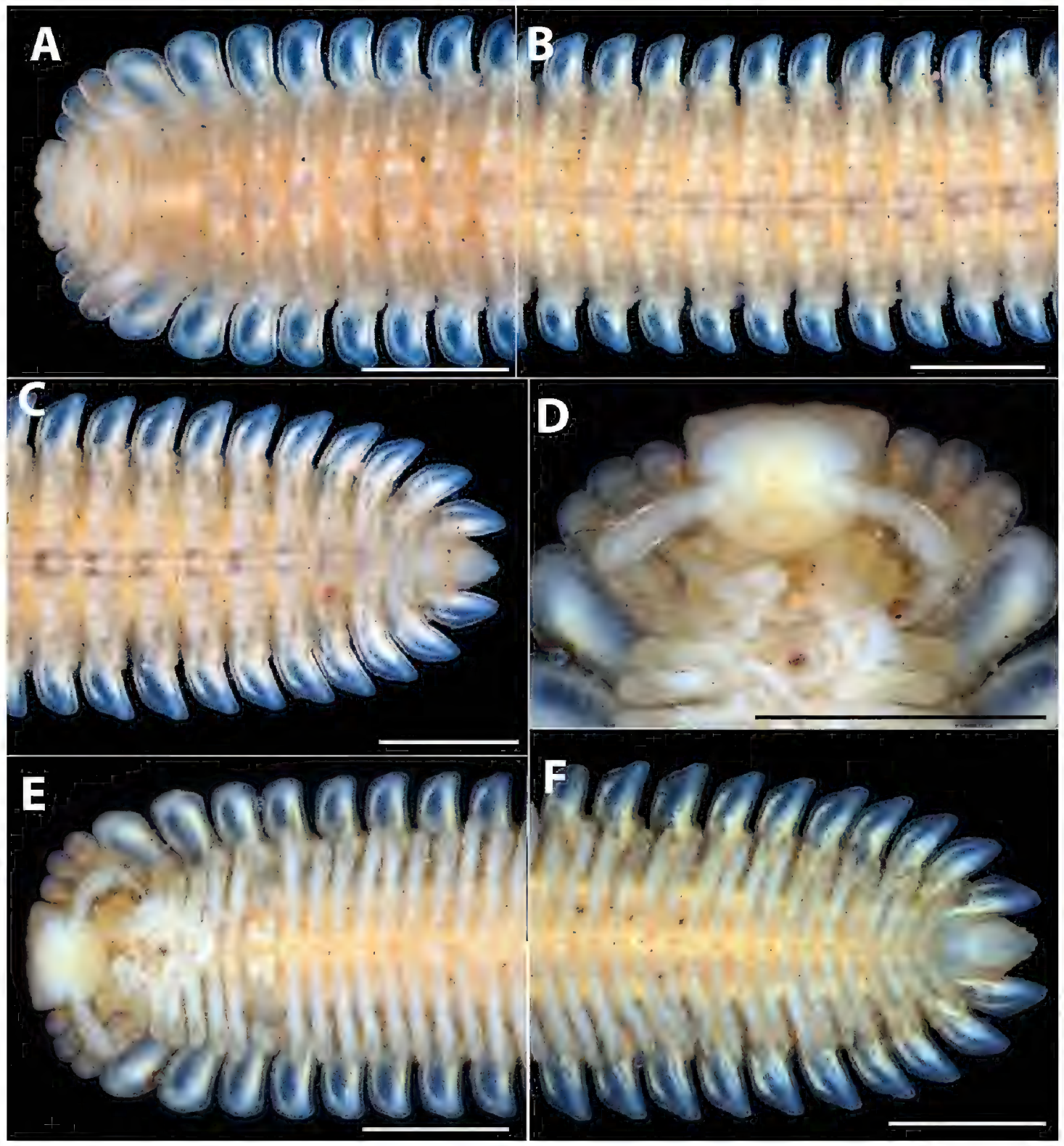

Figure 16. *Pseudodesmus condao* sp. nov. Holotype (IEBR-Myr 982H), under white light. **A.** Anterior part of body, dorsal view; **B.** Midbody body rings, dorsal view; **C.** Posterior part of body, dorsal view; **D.** Head and collum, ventral view; **E.** Anterior part of body, ventral view; **F.** Posterior part of body, ventral view. Scale bars: 1 mm.

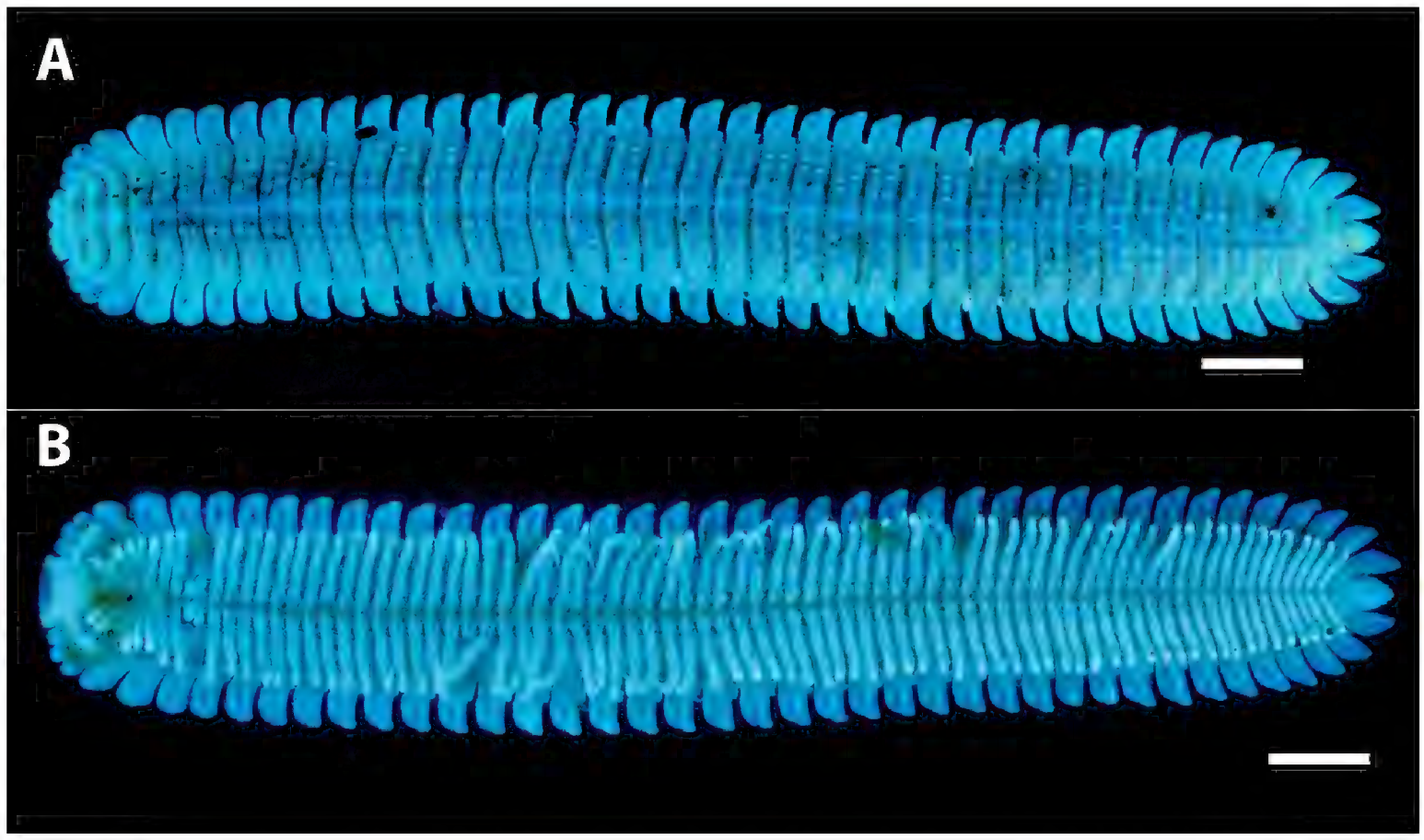

Figure 17. *Pseudodesmus condao* sp. nov. Holotype (IEBR-Myr 982H), under UV light. **A, B.** Habitus, dorsal view (**A**), ventral view (**B**). Scale bars: 1 mm.

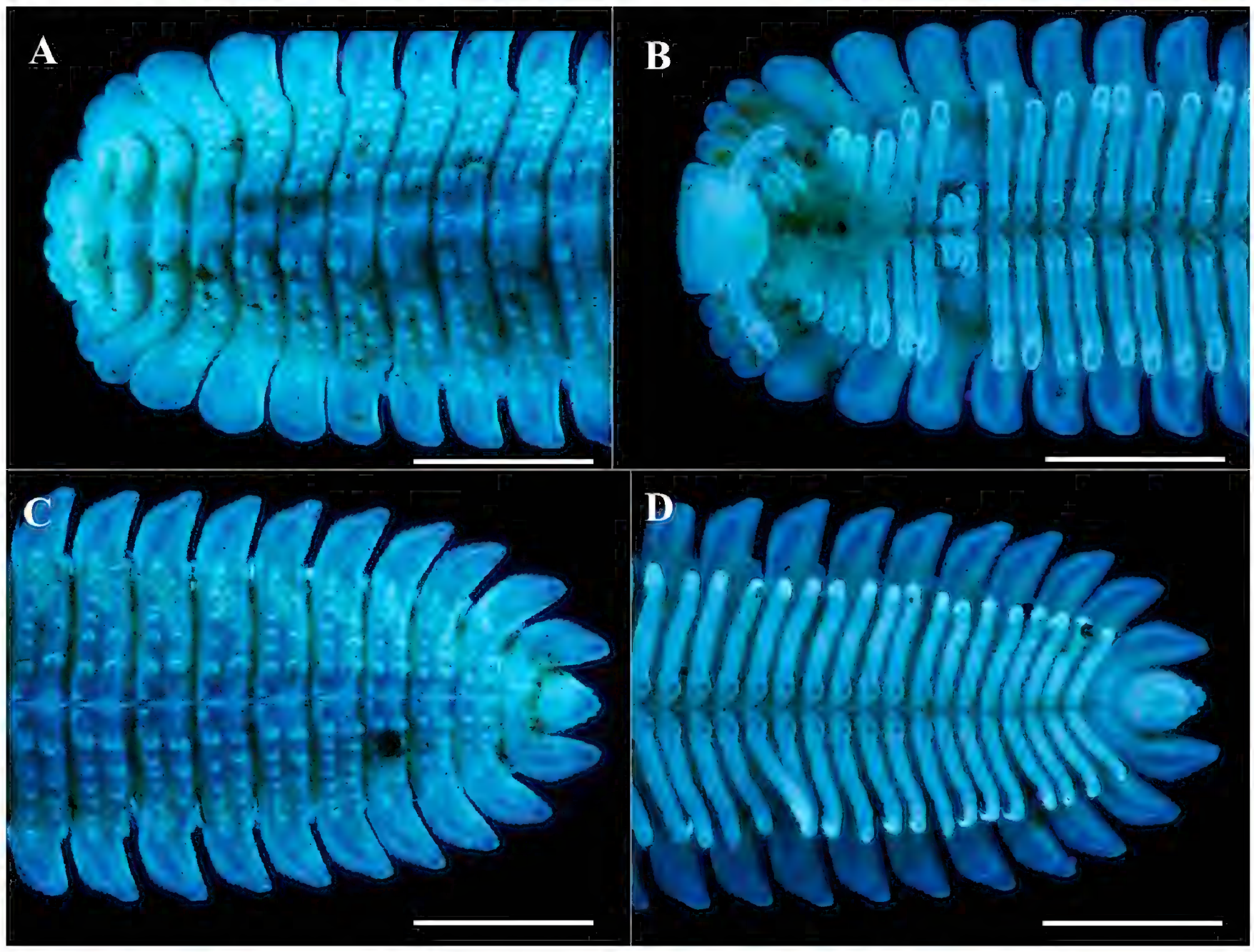

Figure 18. *Pseudodesmus condao* sp. nov. Holotype (IEBR-Myr 982H), under UV light. **A, B.** Anterior part of body, dorsal view (**A**), ventral view (**B**); **C, D.** Posterior part of body, dorsal view (**C**), ventral view (**D**). Scale bars: 1 mm.

In addition, it is smaller than *P. variegatus* and *P. camptotrichus* (length: 9.33 mm vs 32 mm and 14 mm; width: 1.57 mm vs 5.8 mm and 2.0 mm, respestively), having less number of male body rings (42 vs 53–56 and 37–42), and number of metazonal tubercles (two rows of 3–4 + 3–4 and 4–5 + 4–5 tubercles vs two rows of 8–15 + 8–15 and 5–7 + 5–7, and two rows of 6–9 + 6–9 each row, respectively).

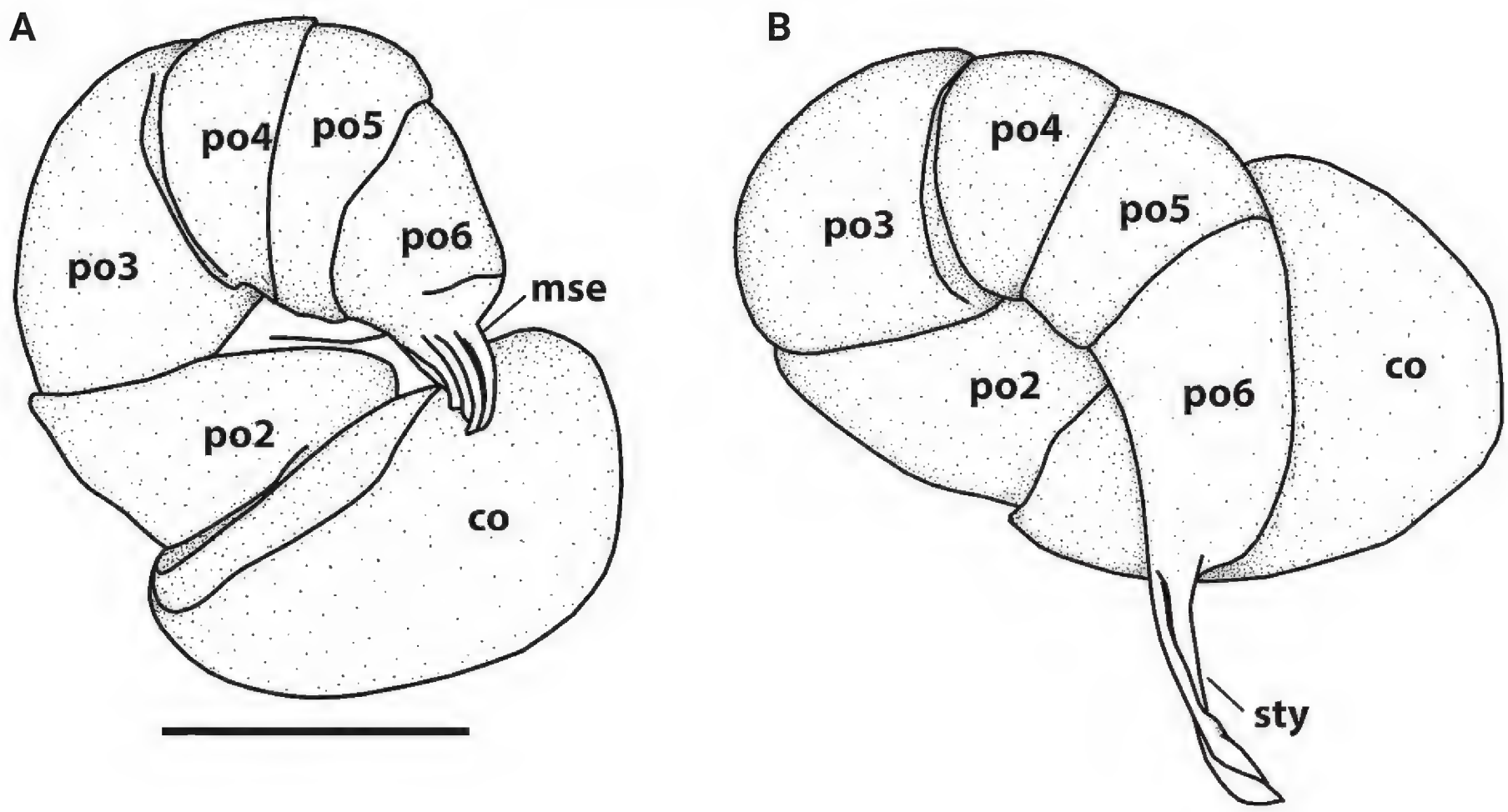

Figure 19. *Pseudodesmus condao* sp. nov. Holotype (IEBR-Myr 982H), gonopods. **A.** Left anterior gonopods, anterior view; **B.** Left posterior gonopod, subventral view. *Abbreviations*: co = coxite = podomere 1; po2 = podomere 2; po3 = podomere 3; po4 = podomere 4; po5 = podomere 5; po6 = podomere 6 (ultimate podomere); mse = macrosetae; sty = stylet. Scale bars: 0.1 mm.

Pseudodesmus condao sp. nov. is differentiated from above three new species, *P. bidoup* sp. nov., *P. ngoclinh* sp. nov and *P. karstomus* sp. nov. in body coloration of generally uniformly dark yellow, smaller body size and number of stylets (two vs four, two and four, respectively).

Description. Male holotype.

Measurements: 42 body rings plus telson, length about 9.33 mm, length of midbody metazona ca. 0.24 mm, width of midbody metazona ca. 1.57 mm, width of midbody prozona ca. 0.63 mm; ratio of width of head and width of collum = 0.89.

Coloration of ethanol-preserved specimens: dark yellow, little darker in the middle.

Head distinctly smaller than collum. Antenna stout, clavate, *in situ* extending to body ring 4; antennomere 6 > 5 >3 > 4 = 2 > 7=1 in length. Collum (Figs 15A, 16A, 17A, 18A) bilobed, each with three anterior lobes, no tubercles. Body rings 2–4 one row of tubercles, then each body ring with 2 rows, body rings 5–8 with 1+1 larger in the middle, then 2+2 larger tubercles, both in anterior and posterior rows (Figs 15A, 16A–C, 17A, 18A, C). Additionally, 2–3 small tubercles in both rows laterally, but only on tergites, not extending to paraterga (Figs 15A, 16A–C, 17A, 18A, C).

Paraterga (Figs 15–18) smooth, almost transparent, wider than in the other species, a little bit spoon form (the distal part is wider than the proximal part), especially in the anterior body ring (up to 10th), later tapering towards the edge, anterior edge is bending backwards, posterior edge remains transverse. Anterior and lateral margin of paraterga serrated (Figs 17A, 18).

Telson (Figs 16C, F, 17C, D) short, caudal margin rounded; epiproct with 2+2 small/tiny tubercles at caudal margin. Paraprocts and hypoproct semi-circular.

Legs slender, shorter than width of body ring together with paraterga, terminating before lateral paratergal margins. Claws normal. Coxal projections present until leg 71 (body ring 38) (Figs 17B, 18D).

Gonopods (Figs 19, 20): Two pairs of gonopods directed anteriad. Anterior gonopods (Figs 19A, 20C, D) 6-segmented, covered with long setae; coxite (*co*) broad, basal part sparsely covered with microgranulations; podomeres 2–5, short and stout; podomere 6 slightly longer than other podomeres, distally carrying macrosetae (*mse*). Posterior gonopods (Figs 19B, 20A, B, E) 6-segmented, covered with sparse long setae; coxite (*co*) broad, basal part sparsely covered with microgranulations; podomeres 2–5 short and stout; ultimate podomere (*po6*) longest, with two apical stylets.

Variation. ***Male paratypes:*** 46–47 body rings plus telson, length about 10.81–11.19mm, length of midbody metazona ca. 0.25–0.28 mm, width of midbody metazona ca. 1.70–1.77 mm, width of midbody prozona ca. 0.75–0.96 mm; ratio of width of head and width of collum = 0.83–0.88. (width of collum: 0.64–0.74 mm, width of head: 0.53–0.65 mm).

Female paratypes: 48–49 body rings plus telson, length about 12.22–12.50 mm, length of midbody metazoan ca. 0.26 mm, width of midbody metazona ca. 1.75–1.77 mm, width of midbody prozona ca. 0.96–0.98 mm; ratio of width of head and width of collum = 0.84. (width of collum: 0.56–0.80 mm, width of head: 0.47–0.67 mm).

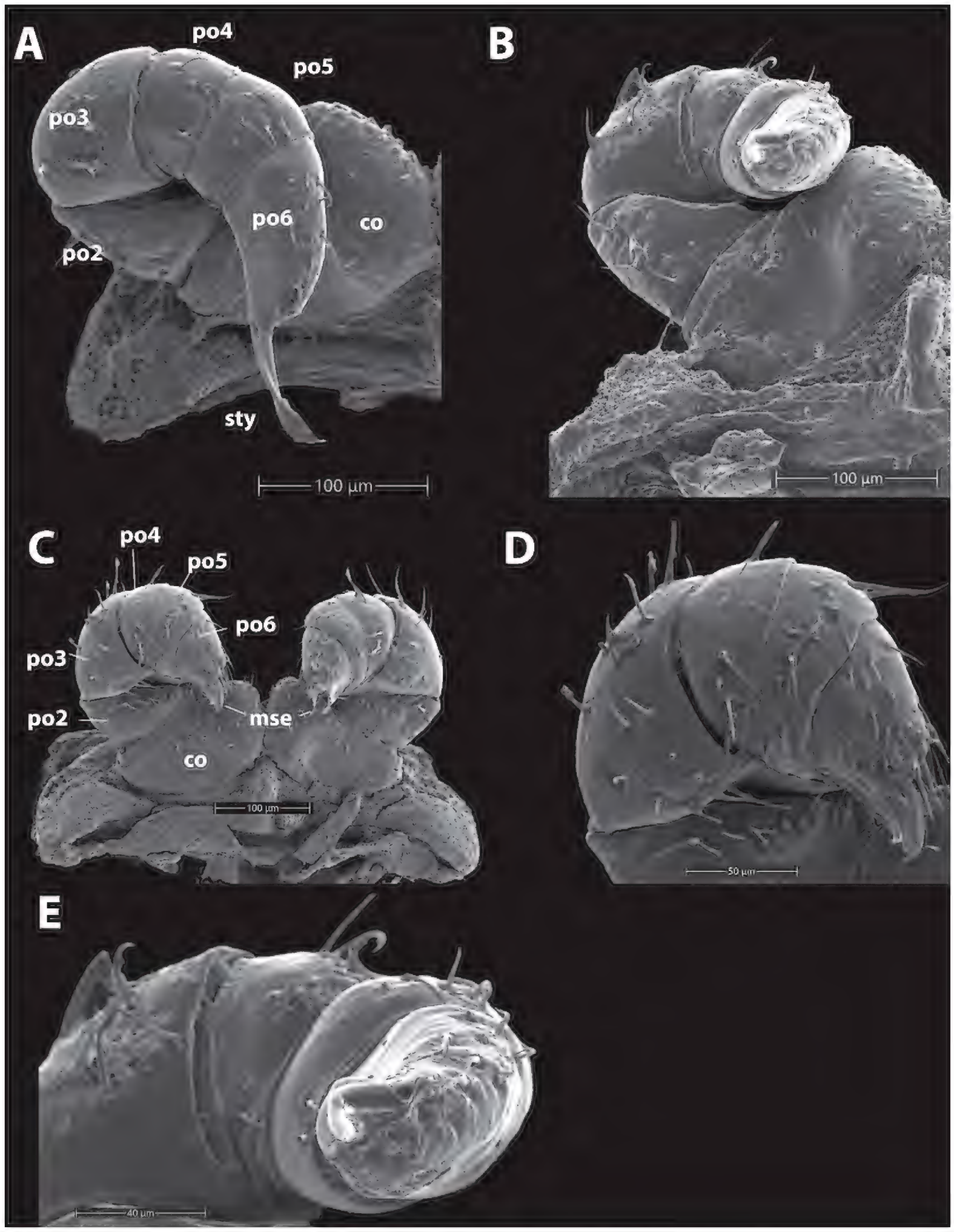

Figure 20. *Pseudodesmus condao* sp. nov. Holotype (IEBR-Myr 982H), gonopods. SEM. **A, B.** Left posterior gonopod, subventral view (**A**), anterior view (**B**); **C.** Anterior gonopods, anterior view; **D.** Left anterior gonopod, anterior view; **E.** Distal part of left posterior gonopod, anterior view. *Abbreviations*: co = coxite = podomere 1; po2 = podomere 2; po3 = podomere 3; po4 = podomere 4; po5 = podomere 5; po6 = podomere 6 (ultimate podomere); mse = macrosetae; sty = stylet.

Etymology. Named after its type locality, Con Dao National Park. Noun in apposition.

Distribution. The species was found in evergreen forests in Con Dao National Park, Ba Ria – Vung Tau Province, southern Vietnam.

DNA barcoding. A fragment of the COI gene is accessioned at NCBI GenBank with the following accession numbers: PQ423226–PQ423227. The new species has a close COI gene similarity with *Gosodesmus claremontus* (JX962723) of 87.46% in the BLAST search.

Pseudodesmus irregularis sp. nov.

https://zoobank.org/2FD3A321-E3F2-419E-A200-4446A132B10A

Figs 21–24

Material examined. ***Holotype.*** Vietnam • 1 male; Khanh Hoa Province, Hon Ba Mt.; 12.11124°N, 108.98426°E; 1,500 m a.s.l.; 15–24 Apr. 2006; A.D. Nguyen leg.; primary forest; IEBR-Myr 958H.

Paratypes. Vietnam • 1 male; same data as for holotype; IEBR-Myr 958P • 1 female; Kon Tum Province,

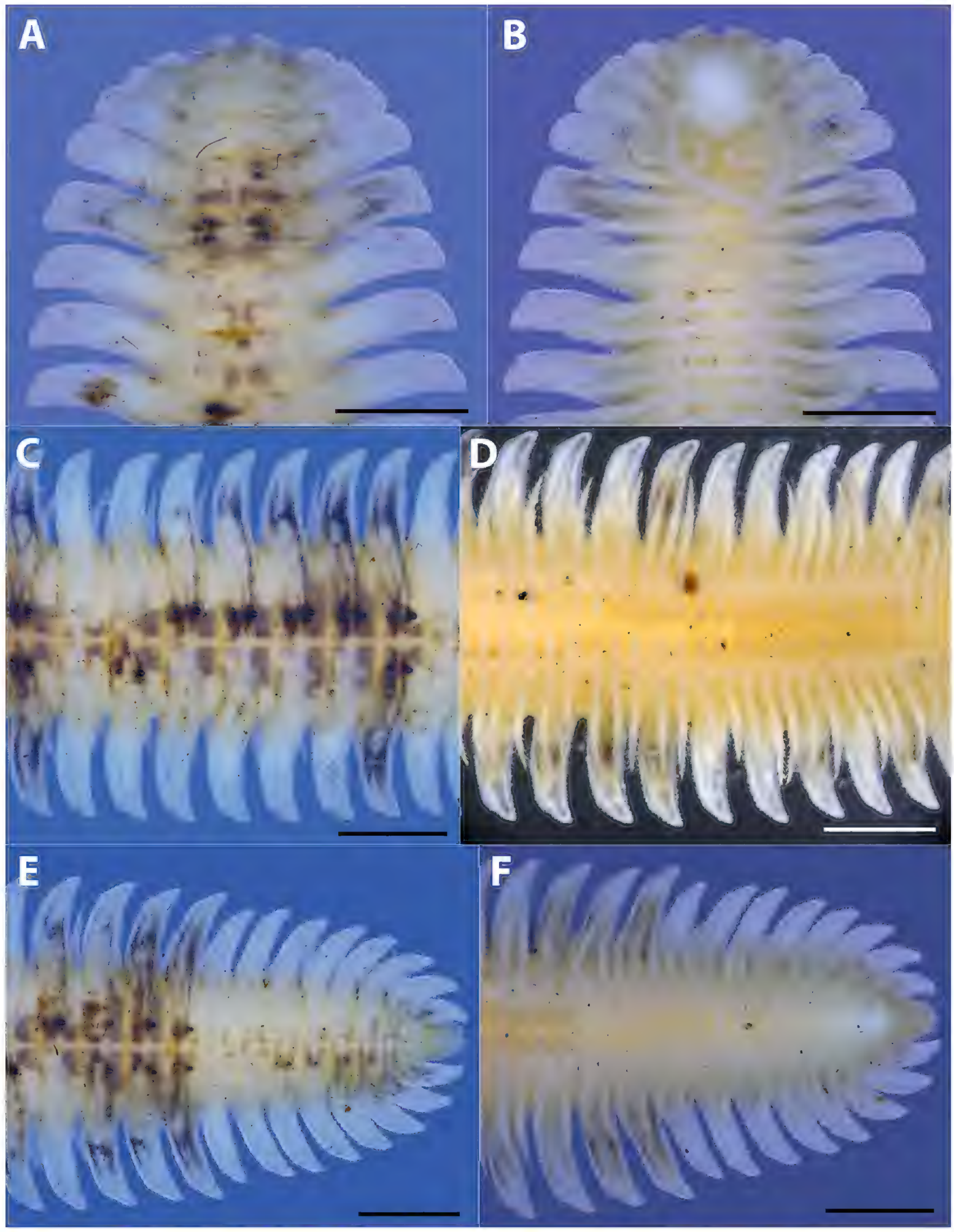

Figure 21. *Pseudodesmus irregularis* sp. nov. Holotype (IEBR-Myr 958H), under normal light. **A, B.** Anterior part of body, dorsal view (**A**), ventral view (**B**); **C, D.** Midbody body rings, dorsal view (**C**), ventral view (**D**); **E, F.** Posterior part of body, dorsal view (**E**), ventral view (**F**). Scale bars: 1 mm.

Ngoc Linh Mt; 15.07071°N, 107.97142°E; 1,700 m a.s.l.; 25 Mar.–11 Apr. 2004, A.D. Nguyen leg.; regenerated forest; IEBR-Myr 960.

Diagnosis. Head narrower than collum. Collum bi-lobed, caudal margin highly elevated with 3+3 tubercles with 3+3 tubercles, and with a row of 1+1 tubercles. Midbody ring with 2 distinct rows of tubercles, anterior row of 6–9+6–9 and posterior of 3+3. Paratergal margins with small/tiny dentations or notches. Posterior gonopods 6-segmented, with three apical stylets.

Diagnosis remarks. The new species is distinguished from *P. camptotrichus* by coloration (irregularly yellow with brown spots vs earth brown), shorter length (12.92 mm vs 14 mm), slightly wider (2.39 mm vs 2.0 mm), having less number of tubercles in posterior metazonal row (3+3 vs 6–9+6–9). The new species is similar to *P. variegatus* regarding body coloration (irregularly yellow with brown spots), but two species can be separated by body size (length: 12.96 mm vs 32 mm; width: 2.39 mm vs 5.8 mm) and and number of metazonal tubercles (two rows of 6–9+6–9 and 3+3 vs two rows of 8–15+8–15 and 5–7+5–7).

Pseudodesmus irregularis sp. nov. is differentiated from above four new species, *P. bidoup* sp. nov., *P. ngoclinh* sp. nov, *P. karstomus* sp. nov. and *P. condao* sp. nov.

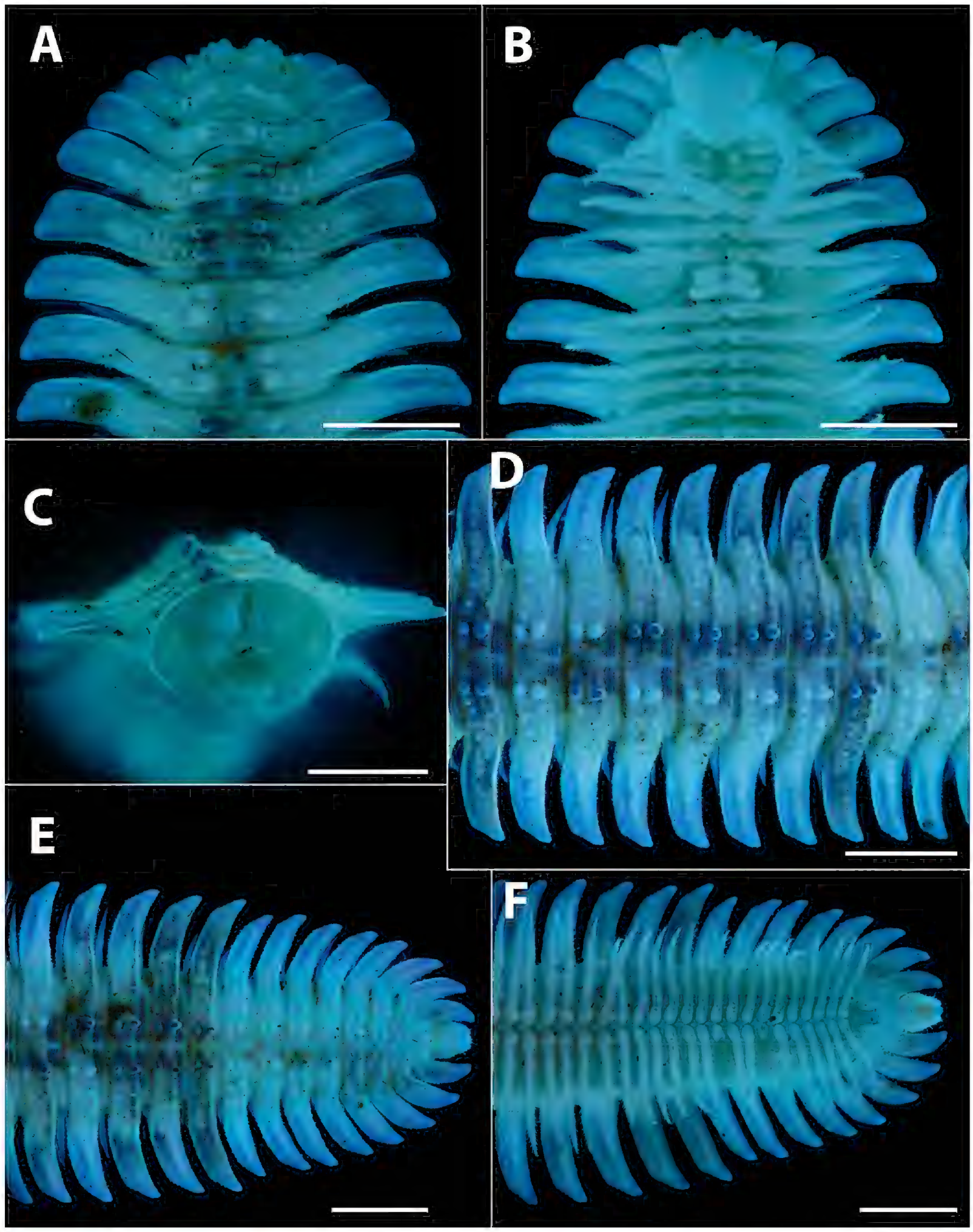

Figure 22. *Pseudodesmus irregularis* sp. nov. Holotype (IEBR-Myr 958H), under UV light. **A, B.** Anterior part of body, dorsal view (**A**), ventral view (**B**); **C.** Cross section of midbody body ring, posterior view; **D.** Midbody body rings, dorsal view; **E, F.** Posterior part of body, dorsal view (**E**), ventral view (**F**). Scale bars: 1 mm.

in body coloration of irregularly yellow with brown spots, body size and number of stylets (three vs four, two, four, and two, respectively).

Description. Male holotype.

Measurements: 42 body rings plus telson, length about 12.96 mm, length of midbody metazona 0.24 mm, width of midbody metazona 2.39 mm, width of midbody prozona 1.08 mm; ratio of width of head and width of collum = 0.74.

Coloration of ethanol-preserved specimens (Fig. 20): complex and irregular: body rings 1–4 with none, body rings 5–7 with 2 brown spots, body ring 8 brown on the right, body ring 9 with two brown spots, body ring 10 brown on the right, body ring 11 brown on the left, body rings 12–13 with two brown spots, body ring 14 none, body ring 15 brown on the left, body rings 16–17 brown on the right, body ring 18 brown on left half, body ring 19 brown on right half, body ring 20 brown on left half, body ring 21 none, body ring 22 with left spot, body ring 23 with two brown spots, body rings 24–26 brown on left half, body rings 27–28 full dark, body ring 29 none, body rings 30–32 brown left, body rings 33–34 brown right,

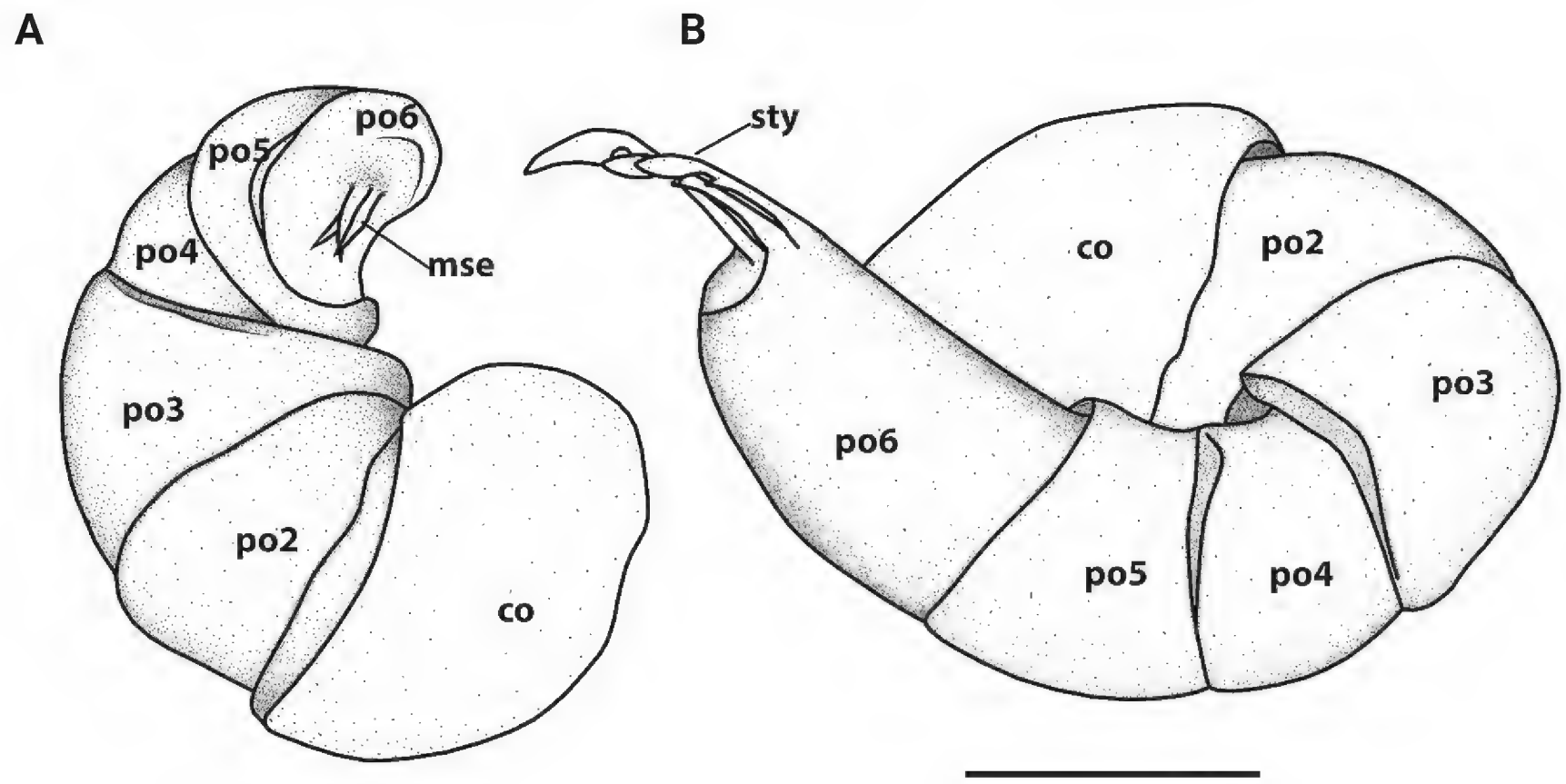

Figure 23. *Pseudodesmus irregularis* sp. nov. Holotype (IEBR-Myr 958H), gonopods. **A.** Left anterior gonopod, anterior view; **B.** Left posterior gonopod, sublateral view. *Abbreviations*: co = coxite = podomere 1; po2 = podomere 2; po3 = podomere 3; po4 = podomere 4; po5 = podomere 5; po6 = podomere 6 (ultimate podomere); mse = macrosetae; sty = stylet. Scale bars: 0.1 mm.

body rings 35–36 full, body rings 37–38 none, body ring 39 brown right, body rings 40–42 light brown.

Head (Figs 21B, 22B) narrower than collum in width, smooth, round-shaped. Antenna stout, clavate, *in situ* extending to body ring 6; antennomere 6 > 5 >3 > 4 = 2 > 7 = 1 in length (Figs 21B, 22B). Collum (Figs 21B, 22B) bilobuled, caudal margin highly elevated with 3+3 tubercles, and with a row of 1+1 tubercles, paramedian one much larger than lateral one.

Body (Figs 21, 22): ring 2 with two rows of 3+3 and 1+1 tubercles; ring 3 with two rows of 3+3 and 3+3 tubercles; other rings with 2 distinct rows of tubercles, anterior row of 6+6 (increasing to (9+9) on midbody rings), and posterior of 2+4 (body ring 4), 3+3 (ring 5), 3+2 (ring 6), 3+3 (on other rings). The last 5 rings with two rows of 3+3 and 3+3 tubercles (Fig. 22E). Anterior rows extending to 2/3 paraterga. Paramedian tubercles on posterior rows much larger than ones on anterior rows.

Paraterga well developed, slightly curved anteriad on body rings 2–3, lateral margins smooth (Figs 21A, B, 22A, B); increasingly less so on the following body rings, slightly curved caudad on body rings 25–27, and strongly curved caudad on body rings 37–40; paraterga of penultimate body ring produced strictly caudad and flanking telson (Figs 21E, F, 22E, F). Lateral margin of paraterga with small/tiny dentations or notches (Figs 21, 22).

Telson (Figs 21E, F, 22E, F) short, caudal margin rounded; epiproct with 2+2 small/tiny tubercles at caudal margin. Paraprocts and hypoproct semi-circular.

Legs slender, shorter than body ring width together with paraterga, terminating before lateral paratergal margins. Claws normal. Coxal sacs strong, present on body rings 3–32 (Fig. 22F).

Gonopods (Figs 23, 24): Two pairs of gonopods directed anteriad. Anterior gonopods (Figs 23A, 24A–C) 6-segmented, covered with long setae; coxite (*co*) broad, basal part sparsely covered with microgranulations; podomeres 2–5, short and stout; podomere 6 slightly longer than other podomeres, distally carrying macrosetae (*mse*). Posterior gonopods (Figs 23B, 24D–F) 6-segmented, covered with sparse long setae; coxite (*co*) broad, basal part sparsely covered with microgranulations; podomeres 2–5 short and stout; ultimate podomere (*po6*) longest, with three apical stylets (*sty*).

Variation. ***Male paratype*** **(IEBR-Myr 958P)**: 36 body rings plus telson, length about 9.75 mm, length of midbody metazoan ca. 0.14 mm, width of midbody metazona ca. 1.72 mm, width of midbody prozona ca. 0.82 mm; ratio of width of head and width of collum = 0.85.

The female from Ngoc Linh Mts (**IEBR-Myr 960**) has 41 body rings plus telson; midbody width 2.1 mm, length about 10.11 mm. Coloration with widening pattern repeated between 7–12, 13–17, 18–24, 25–31, 32–36 body rings (see also Enghoff 2011). Tubercles are small: on collum only one row, on 2–4 two weak rows (reaching only one row on paraterga), from body ring 5 onwards two rows, each 1+1 large tubercles in the middle, then anterior row 10–13 small tubercles reaching edge of paraterga, in posterior row only 3–4 small tubercles, on the last five body rings anterior row is weaker but still with 8–10 small tubercles, in posterior row the median tubercles larger, with 4 small tubercles laterally.

Etymology. To emphasize the irregular pattern of terga. Noun in apposition.

Distribution. The species has been only known from Khanh Hoa and Kon Tum Province, southcentral Vietnam.

DNA barcoding. Sequencing a fragment of the COI gene failed.

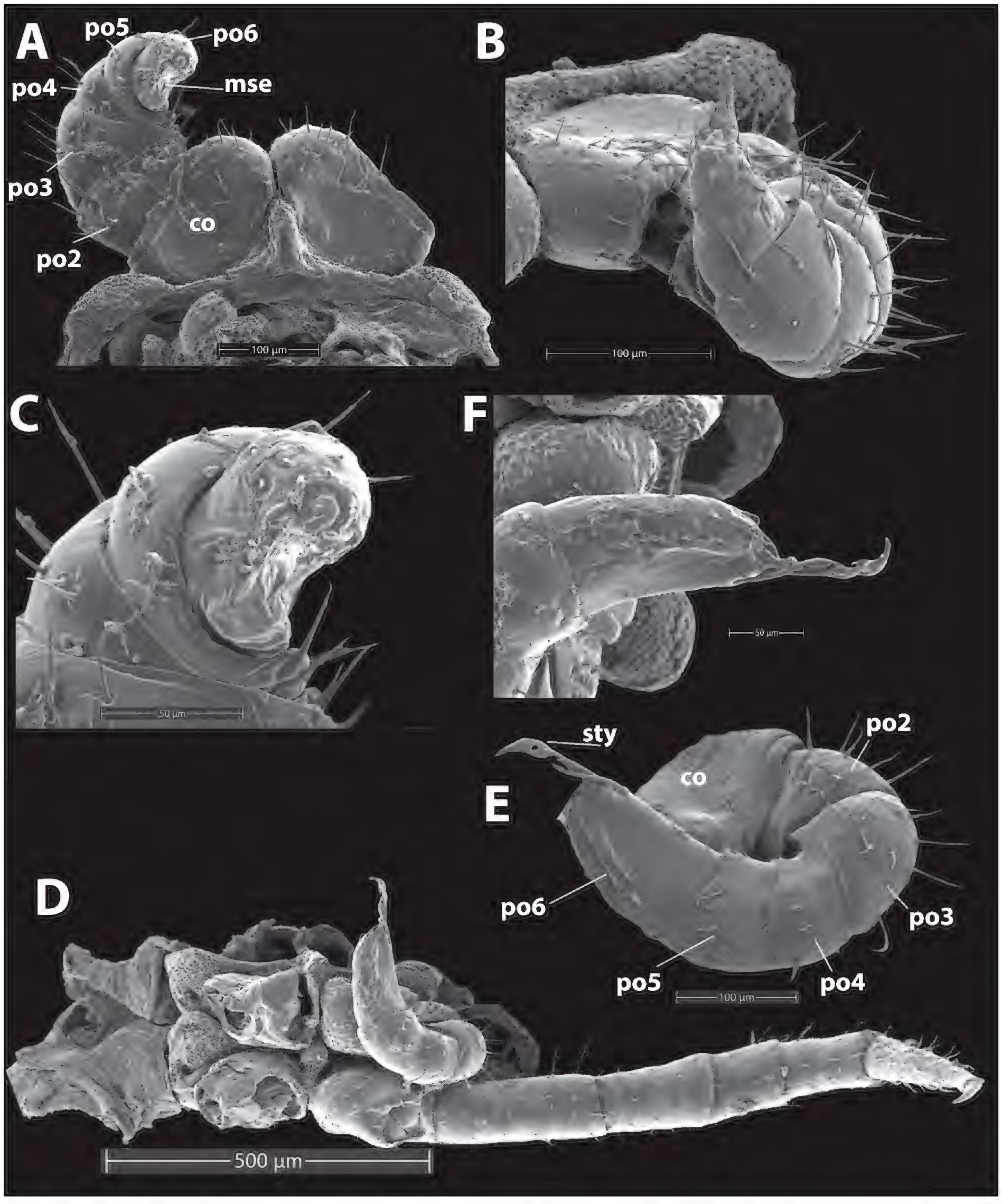

Figure 24. *Pseudodesmus irregularis* sp. nov. Holotype (IEBR-Myr 958H), gonopods. SEM. **A, B.** Left anterior gonopod, anterior view (**A**), ventral view (**B**); **C.** Distal part of left anterior gonopod, anterior view; **D, E.** Posterior gonopod and leg 11, ventral view (**D**), sublateral view (**E**); **F.** Distal part of posterior gonopod, ventral view. *Abbreviations*: co = coxite = podomere 1; po2 = podomere 2; po3 = podomere 3; po4 = podomere 4; po5 = podomere 5; po6 = podomere 6 (ultimate podomere); mse = macrosetae; sty = stylet.

Pseudodesmus spp.

The following specimens have peculiar body shape and color pattern, but because we have only females, we refrained to describe them as new species.

Pseudodesmus sp. 1

Fig. 25

Material examined. Vietnam • 02 females; Daklak, Mdrak, Chu Mur; 12.71233°N, 108.86092°E, 478 m

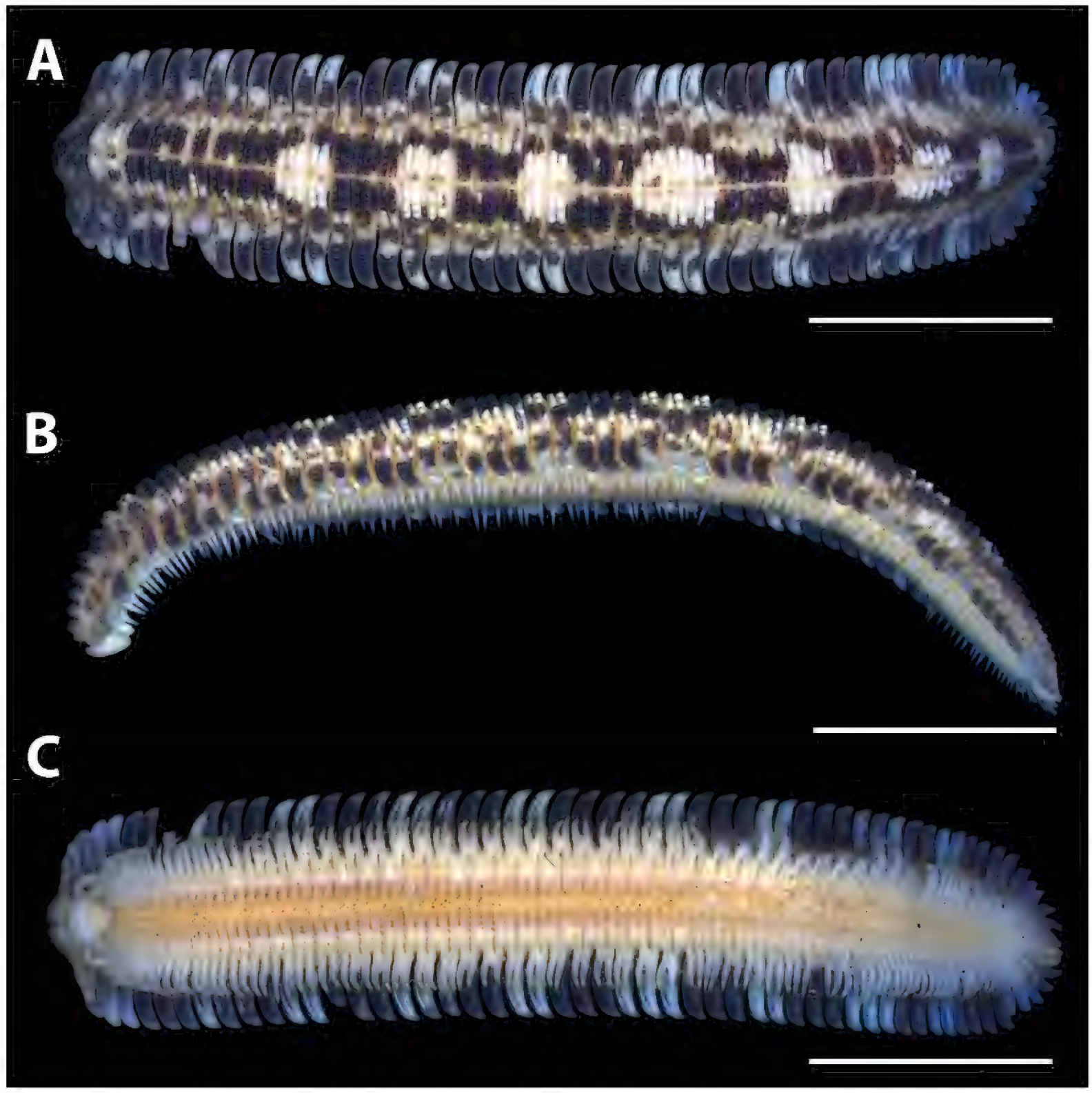

Figure 25. *Pseudodesmus* sp.1. Female (IEBR-Myr 875). **A–C.** Habitus, dorsal view (**A**), lateral view (**B**), ventral view (C). Scale bars: 5 mm.

a.s.l., 15 Jul. 2019; Hoang Quang Duy leg.; under decaying wood along a trail; IEBR-Myr 875.

Description. ***Measurements:*** 57 and 64 body rings (midbody width of the larger one 3.9 mm).

Collum is unique, bilobed, but also divided to anterior and posterior ridges with 5–6+5–6 small tubercles in both rows. Legs with small coxal sacs. Tubercles in two rows, medially widely separated, 2+2 median tubercles not especially large, anterior row with 5–6+5–7 tubercles extending to the middle/edge or paraterga, posterior row with 5–6 small tubercles.

Coloration of ethanol-preserved specimens: very strong pattern, symmetric dark brown (almost black) color extends to the paraterga as well. Dark paraterga: 2–5, 8–10, 14, 18–19, 23, 26–29, 33–34, 36–38, 41–43, 46, 50–51, 53–54, 57–58, 61–64.

Pseudodesmus sp. 2

Fig. 26

Material examined. VIETNAM • 1 female; Quang Binh Province, Bo Trach Dist., Son Doong cave, outside cave, back entrance; 17.48667°N, 106.28500°E; 16 Jan. 2023; A.D.Nguyen leg.; IEBR-Myr 987.

Description. ***Measurements:*** 55 body rings plus telson, length ca. 10.9 mm, midbody width 2.7 mm.

Quite convex body, almost cylindrical (without paraterga).

Collum bilobed, narrow, a little bit narrower than head, 2 pair of tubercles, posterior ones stronger.

Tergite tubercles on body rings 2–7 strong and wide, but from there onwards decreasingly inconspicuous, from 8th backwards terga are clearly divided in anterior and posterior parts, also by coloration: light anterior part wider, light posterior part a bit narrower, tubercles disappearing, only weak transversal ridges appear. Telson, including para- and hypoproct dark brown. Coxal sacs on legs small, weak.

Color of ethanol-preserved specimens unique: dark thin median line, terga broadly light, almost white, base of all paraterga dark brown, edge of paraterga light yellow: in general looks like three longitudinal dark stripes, one thin median line and two wider parallel brown stripes. Head color is different: two white bumps (almost like large compound eyes), frontale and mandibulae dark brown, antennae dark brown.

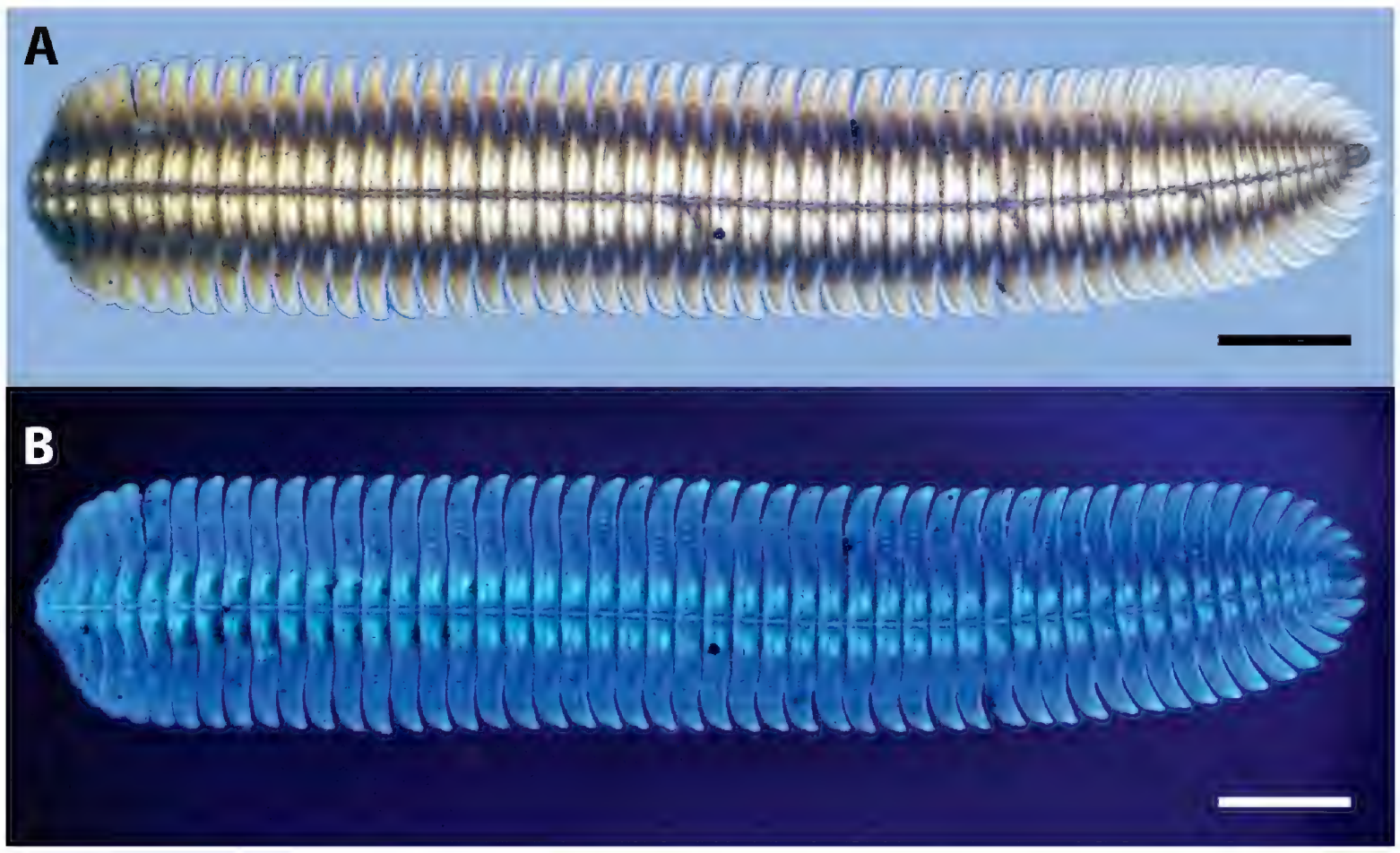

Figure 26. *Pseudodesmus* sp.2. Female (IEBR-Myr 987). **A, B.** Habitus, dorsal view, under normal light (**A**), dorsal view, under UV light (**B**). Scale bars: 1 mm.

Molecular analysis

Dataset

Because of length variation and noisy ends, the final aligned COI dataset comprised a 573 bp fragment from 15 platydesmidan specimens including an outgroup specimen, *Andrognathus corticarius* Cope, 1869 (Table 1). The nucleotide frequencies of A, T, G, and C were 31.1%, 38.5%, 14.6%, and 15.8%, respectively. The GC content was 30.4%. The dataset contained 186 (32.5%) parsimony informative and 251 (43.8%) variable sites.

Genetic distance

The average K2P distance between the 15 platydesmidan samples was 18.0% ± 1%. The genetic distance between the outgroup (*Andrognathus corticarius*) and other andrognathid species was from 22.9% to 32.0%. The distance between platydesmid genera varied between 13.8% (*Pseudodesmus* and *Gosodesmus*) to 27.3% (*Pseudodesmus* and *Brachycybe*). The interspecific distance varied from 1.6% (*P. karstomus* sp. nov.) to 3.6% (*P. ngoclinh* sp. nov.) (Table 2). The genetic distance between new species varied from 14.4%–14.6% (*P. condao* sp. nov. and *P. karstomus* sp. nov.) to 15.1%–17.7% (*P. ngoclinh* sp. nov. and *P. karstomus* sp. nov.).

Phylogenetic relationship

A phylogenetic tree was reconstructed for the 573 bp dataset using maximum likelihood analysis (Fig. 27). The tree supports the separation of two new species, *P. ngoclinh* and *P. karstomus*, from their congeners, with bootstrap values (97% and 88%, respectively). The other new species, *P. condao*, is clustered within a clade consisting of *Brachycybe*, *Gosodesmus*, and *Yamasinaium*, with a low bootstrap value (49%). However, the relationship between those three genera is poorly supported (51–57%). Perhaps, the 573 bp fragment of the COI is too short to accurately estimate phylogenetic relationships.

A key to *Pseudodesmus* species in Vietnam

1 Head slightly broader than collum (ratio of width of head and width of collum = 1.05) ..... *P. ngoclinh* sp. nov.
– Head narrower than collum 2
2 Head significantly narrower than collum (ratio of width of head and width of collum = 0.74–0.89) 3
– Head slightly narrower than collum (ratio of width of head and width of collum = 0.93–0.98) 4
3 Body smaller (length about 9.33 mm, width of midbody metazona ca. 1.57 mm); midbody metazonae with two rows of 3–4+3–4 large and 4–5+4–5 large tubercles; posterior gonopod with two distal stylets ..... *P. condao* sp. nov.
– Body larger (length about 12.96 mm, width of midbody metazona 2.39 mm); midbody metazonae with two rows of 6–9+6–9 and 3+3 tubercles; posterior gonopod with three distal stylets ..... *P. irregularis* sp. nov.
4 Body coloration rather uniformly earth brown ..... *P. camptotrichus*
– Body coloration not uniform, somewhat irregular distribution of yellow-brown and black spots) 5

5 Body larger (length about 32.0 mm, width of midbody metazona 5.8 mm); midbody metazonae with two rows of 8–15+8–15 and 5–7+5–7 ..... *P. variegatus*

– Body smaller; midbody metazonae with two rows of tubercles, but different in number 6

6 Ratio of body length and midbody width about 4.6; midbody metazonae with two rows of 7–8+7–8 and 2+2 tubercles *P. karstomus* sp. nov.

– Ratio of body length and midbody width about 5.7; midbody metazonae with two rows of 5+5 and 3+3 tubercles ..... *P. bidoup* sp. nov.

Table 1. Voucher specimens and GenBank accession numbers.

No	Species	Species code	Locality	GenBank Accession Number	Sources
1	*Pseudodesmus* sp.1	IEBR-Myr 875	Vietnam, Daklak Province, Mdrak, Chu Mur	PQ423228	This study
2	*Pseudodesmus condao* sp. nov.	IEBR-Myr 982	Vietnam, Ba Ria–Vung Tau Province, Con Dao NP	PQ423226	
3	*Pseudodesmus condao* sp. nov.	IEBR-Myr 977	Vietnam, Ba Ria–Vung Tau Province, Con Dao NP	PQ423227	
4	*Pseudodesmus ngoclinh* sp. nov.	IEBR-Myr 986a	Vietnam, Kon Tum Province, Ngoc Linh Mts,	PQ423222	
5	*Pseudodesmus ngoclinh* sp. nov.	IEBR-Myr 986b	Vietnam, Kon Tum Province, Ngoc Linh Mts,	PQ423223	
6	*Pseudodesmus karstomus* sp. nov.	IEBR-Myr 959a	Vietnam, Cao Bang Province, Tra Linh District	PQ423224	
7	*Pseudodesmus karstomus* sp. nov.	IEBR-Myr 959b	Vietnam, Cao Bang Province, Tra Linh District	PQ423225	
8	*Yamasinaium* sp.	IEBR-HNMH	Japan, Okinawa	PQ423229	
9	*Brachycybe producta*	MIL0021	U.S.A.	JX962721	Marek et al. (2012)
10	*Brachycybe lecontii*	–	U.S.A.	JX437064	Brewer et al. (2013)
11	*Brachycybe rosea*	MIL0025	U.S.A.	JX962722	Marek et al. (2012)
12	*Gosodesmus claremontus*	SPC000941	U.S.A.	JX962723	Marek et al. (2012)
13	Andrognathidae sp.	FLMNH 42128	Myanmar	MF983566	GenBank (direct submission)
14	Andrognathidae sp.	FLMNH 42103	Myanmar	MF983567	GenBank (direct submission)
15	*Andrognathus corticarius*	VTEC MPE01938	U.S.A.	MH282831	Shorter et al. (2018)

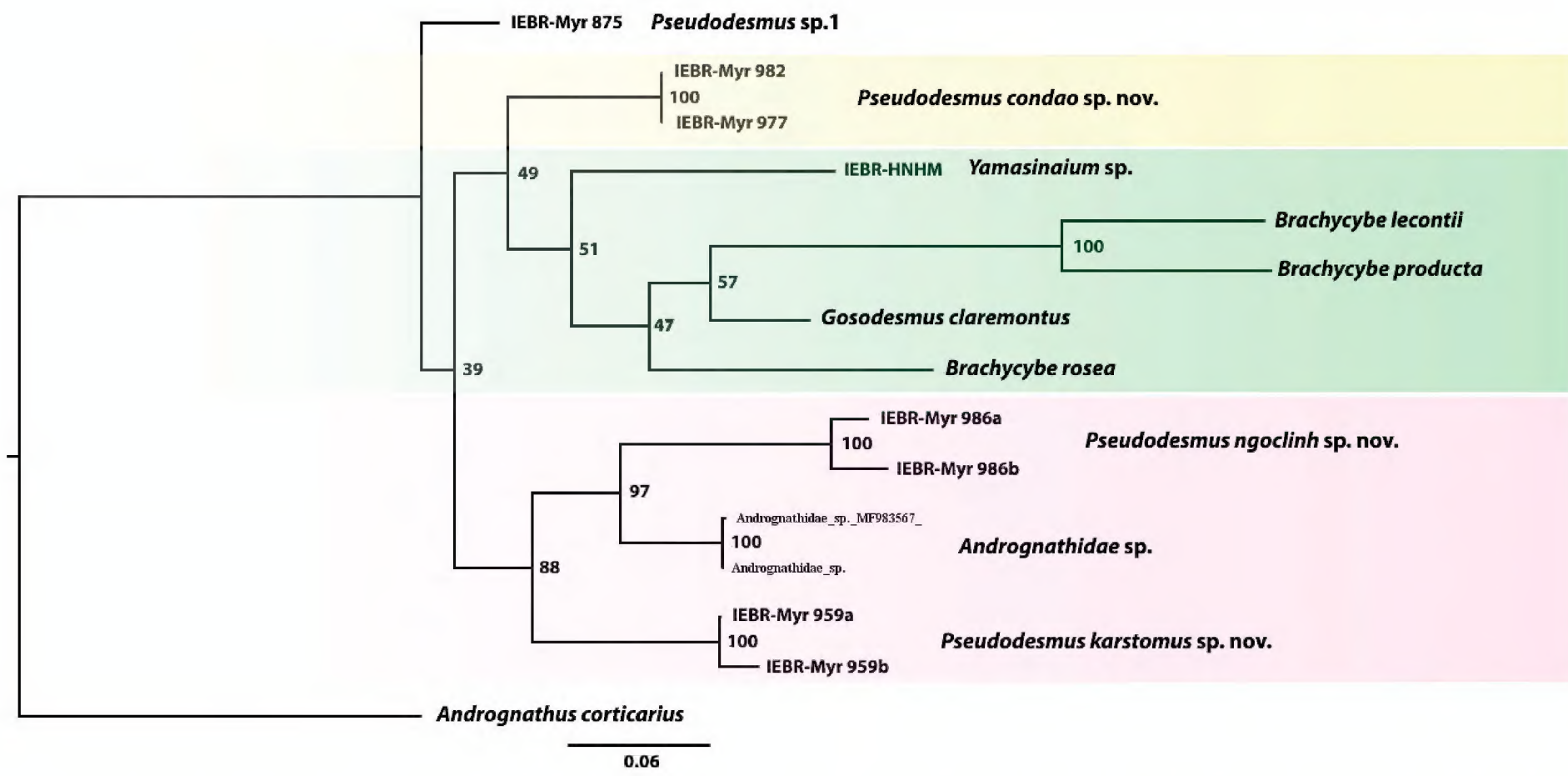

Figure 27. Phylogenetic diagram inferred from a 573bp fragment of the COI gene using maximum likelihood analysis. Numbers at node are bootstrap values.

Table 2. Pairwise nucleotide difference (Kimura 2-parameter model) over sequence pairs between species. Numbers in bold are intraspecific divergences.

Species	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
(1) *Pseudodesmus ngoclinh* sp. nov. (IEBR-Myr 986a)														
(2) *Pseudodesmus ngoclinh* sp. nov. (IEBR-Myr 986b)	**0.036**													
(3) *Pseudodesmus karstomus* sp. nov. (IEBR-Myr 959a)	0.170	0.151												
(4) *Pseudodesmus karstomus* sp. nov. (IEBR-Myr 959b)	0.177	0.158	**0.016**											
(5) *Pseudodesmus condao* sp. nov. (IEBR-Myr 982)	0.177	0.170	0.144	0.146										
(6) *Pseudodesmus condao* sp. nov. (IEBR-Myr 977)	0.177	0.170	0.144	0.146	**0.000**									
(7) *Pseudodesmus* sp.1 (IEBR-Myr 875)	0.168	0.159	0.123	0.127	0.101	0.101								
(8) Androgna thidae sp. (MF983567)	0.121	0.117	0.127	0.131	0.144	0.144	0.125							
(9) Androgna thidae sp. (MF983566)	0.119	0.115	0.125	0.131	0.142	0.142	0.125	0.002						
(10) *Yamasinaium* sp. (IEBR-HMNH)	0.227	0.220	0.179	0.179	0.150	0.150	0.131	0.185	0.185					
(11) *Gosodesmus claremontus* (JX962723)	0.199	0.192	0.165	0.172	0.138	0.138	0.142	0.152	0.150	0.161				
(12) *Brachycybe rosea* (JX962722)	0.213	0.213	0.181	0.190	0.165	0.165	0.161	0.179	0.176	0.155	0.140			
(13) *Brachycybe producta* (JX962721)	0.268	0.273	0.248	0.260	0.208	0.208	0.234	0.248	0.246	0.246	0.185	0.215		
(14) *Brachycybe lecontii* (JX437064)	0.273	0.273	0.248	0.263	0.212	0.212	0.236	0.246	0.243	0.222	0.187	0.210	0.133	
(15) *Androgna thus corticarius* (MH282831)	0.320	0.312	0.258	0.263	0.258	0.258	0.229	0.248	0.246	0.266	0.263	0.283	0.294	0.301

Discussion

Located in tropical regions, Vietnam is expected to have a great diversity of millipedes (Enghoff et al. 2004). Like other millipede taxa e.g. Callipodida (Nguyen et al. 2023), Polydesmida (Nguyen et al. 2024), the Platydesmida have been poorly known, with a little information since 1953. The discoveries of five new species are remarkable for the millipede fauna of Vietnam, but the number of platydesmidan species (seven) does not reflect the true diversity of millipedes in Vietnam. More intensive surveys, especially in caves, will reveal more new species.

The relation or position of *Pseudodesmus* within Androgna thidae was previously discussed several times but no detailed study has been carried out so far. In the gonopods, Carl (1912) didn't find any differences between *Pseudodesmus tuberculatus* and the species of *Platydesmus* and *Brachycybe*, and he proposed *Brachycybe* to be an intermediate form between *Platydesmus* and *Pseudodesmus*.

Gardner (1975) in his Nearctic revision of the family Androgna thidae stated that the species can be superficially divided into two main groups. The first group has broad body (up to 4 mm in width) including *Brachycybe*, *Sinocybe* and *Pseudodesmus*, and the second one has more vermiform bodies comprising of four (North American) genera *Ischnocybe*, *Mitocybe*, *Gosodesmus* and *Androgna thus*. These two groups formally belong to two subfamilies Bazillozoniinae and Dolisteninae, respectively (Hoffman 1980). Hoffman (1980) kept *Pseudodesmus* and *Sinocybe* separate, but he also said "I am by no means assured that *Sinocybe* can be distinguished from *Pseudodesmus*" (Hoffman 1980: p. 117). Also, he wrote that "it is difficult to distinguish *Platydesmus* from *Brachycybe*", even though he classified them into different families (Platydesmidae *vs* Androgna thidae (Hoffman 1980).

Later, Shelley et al. (2005) considered *Sinocybe* to be a junior synonym of *Brachycybe*. Furthermore, they said that there are few if any structural differences between *Brachycybe* and *Pseudodesmus*, and the two genera could be synonymized, and *Yamasinaium* can also be a candidate under *Brachycybe* (Shelley et al. 2005).

Decker (2014) in a conference presentation tentatively suggested synonymy of *Brachycybe* and *Pseudodesmus*, but his detailed reasons are still in manuscript (Decker pers. comm.). He generally said: "Due to the similarity and the mosaic like pattern of morphological characters (incl. gonopods) sharing with North American *Brachycybe*, all Southeast Asian members of Andrognathidae were placed for the present under *Brachycybe*" (Decker 2014). His classificatory acts should be invalid as it was presented only in a conference poster.

Phylogenetically, members of the genera, *Brachycybe* and *Pseudodesmus*, are not monophyletic and occur in distinct clades, but the tree is poorly supported (39%, Fig. 27). In the tree, *Brachycybe* is more closely related to *Gosodesmus*, however, this result should be contrasted with the phylogeny of Rodriguez et al. (2018) who reported that *Brachycybe* was related to *Platydesmus*, and the non-monophyly of the family Andrognathidae. The position of *Yamasinaium* and *Gosodesmus* on the tree, however, is a little bit strange, considering that with they have long and slender body shapes and belong to the subfamily Dolisteninae. Additionally, the geographical distribution of the three genera may also be viewed as problematic: the monotypic *Gosodesmus* (*G. claremontus* Chamberlin, 1922) is from the western U.S.; *Brachycybe* has a northern temperate distribution mainly in southeastern and western United States (6 species), but it has also species in Japan, South Korea, central China, and Taiwan (3 species) (Shelley et al. 2005; Mikhaljova et al. 2010; Shelley and Golovatch 2011; Brewer et al. 2012); *Yamasinaium*, on the other hand, is confined to East Asia: the Korean Peninsula, southern Japan, and Taiwan (3 species).

Pseudodesmus species are only recorded in tropical habitats of Southeast Asia (Brewer et al. 2012). Due to the geographical distribution and the weak molecular supports, it may be better to keep all these genera, especially *Brachycybe* and *Pseudodesmus*, separate. The synonymy of those two genera needs to be confirmed with more morphological and molecular evidence.

As mentioned above, the used fragment of the COI may be too short for phylogenetic analysis. It may not suitable for the reconstruction of relationship between species and genera solely based on the COI, as it is not able to resolve deeper nodes/early splits. However, it is a great tool to identify species and the phylogeny nicely shows clusters of specimens belonging to the same species and visualizes the genetic distances (Fig. 26).

Acknowledgements

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